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(*Recognosce notum, ignotum inspice*)

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VOLUME XXII AUGUST 1938 NOS. 1 & 2

TUNBRIDGE WELLS FORAY

22–26 *May*, 1936

By J. RAMSBOTTOM

A fairly large party assembled at the Headquarters, Castle Hotel, Tunbridge Wells, on Friday, May 22nd. As several members arrived somewhat late, the only business done in the evening was the explaining of the general arrangements for the foray, which had been made by Mr A. A. Pearson to whom all the members present were greatly indebted for all he did to make the foray a success.

The weather had been very dry for some weeks and was exceptionally fine over the week-end; the ideal of abundant rain followed by a fine week-end is unfortunately beyond the achievement of even the most efficient foray secretary.

On Saturday the party proceeded to Sheffield Park, Fletching, Sussex. The attractive gardens were visited, where there was a brilliant mass of Japanese Primulas and an abundance of interesting trees and shrubs. Sheffield Park has both literary and sporting associations. Edward Gibbon spent much time there in the company of his friend and patron John Baker Holroyd, the first Lord Sheffield; his remains are in the near-by church. Several of us were perhaps more interested in seeing the famous cricket ground where under the patronage of the third Earl* the first match of visiting Australian teams was played for many years. One of the lakes which in the hard winter of 1890–1 had ice thick enough for several cricket matches to be played on it, was covered at the time of our visit with "water bloom".

Fungi were as scarce as we had feared; *Amanita pantherina* and *Corticium caeruleum*, were among the few larger fungi found and *Tilletia striiformis*, *Urocystis Anemones*, *Hypocrea pulvinata* and *Stagnospora Curtisii* among the microfungi.

After returning to Headquarters a visit was paid to the Tunbridge Wells Municipal Museum where we were received by the honorary Curator, Dr J. C. M. Given. The chief object of the visit was to see the very fine exhibit of Tunbridge ware. In preparing this, thin strips of differently coloured woods are assembled into a block, so that their ends display the desired pattern or picture. They are then glued and bound together under pressure and the mass is cut transversely into thin strips with a circular saw. This "veneer" is glued on to the table, box, or other article to be decorated, then carefully smoothed and polished. The interest to the mycologist is that the "green wood" is oak infected with the mycelium of *Chlorosplenium aeruginosum*.

In the evening the place for the next spring foray was discussed. Votes of thanks were passed to the various landowners and especial thanks to Mr A. A. Pearson for his arrangements.

Brockhurst Park was visited on Saturday. The Rhododendrons in the drive were heavily infected with *Sporocybe Azaleae* and some very large specimens of *Reticularia Lycoperdon* attracted some attention. But intensive search failed to add many species even of microfungi, though there was abundance of *Monilia aurea*. At the spot where we lunched in an open field, lightning had struck an oak and for twenty to twenty-five feet the rift was lined with *Coniophora puteana*.

After tea Messrs Wallace's nurseries were visited.

Monday was again a glorious day and Harriss Rocks and Eridge were explored. The former produced the beautiful *Arachnopeziza aurelia*, *Urceolella versicolor*, and

* He presented the well-known cricket trophy, the Sheffield Shield, to be competed for annually between Victoria, New South Wales, and South Australia.

Elaphomyces granulatus; the latter an old whitened specimen of *Polyporus sulphureus* covered with the rusty brown *Acrostalagmus cinnabarinus* and *Fomes annosus* growing on beech. But on the damp rocks there was growing in quantity the filmy fern *Hymenophyllum tunbridgense*, first "found by Dr Dare" (Ray, *Historia*, 1 (1686), 141). It was at Eridge Park that Lord North, recuperating from the court life of James I, discovered a chalybeate spring, consulted experts and started the fashion of drinking the waters which made Tunbridge Wells famous as a resort.

To end the day's foray High Rocks was visited; this was merely a trip to see the best known examples of the Hastings sandstone outcrops of the neighbourhood, but *Pluteus cervinus* was added to the list.

After tea a visit was paid to Messrs Constable's nursery.

All members present contributed to the list of fungi. Mr T. Petch supplied the list of Mycetozoa.

S. = Sheffield Park; *B.* = Buckhurst Park; *H.* = Harriss Rocks; *E.* = Eridge.

HYMENOMYCETES

Amanita pantherina (DC.) Fr., *S.*, rubescens (Pers.) Fr., *B.*
Armillaria mellea (Vahl) Fr., *S.*
Marasmius conigenus (Pers.) Karst., *S.*, dryophila (Bull.) Karst., *B.*
Panus stipticus (Bull.) Fr., *S.*
Pluteus cervinus (Schaeff.) Fr., High Rocks.
Galera siligvinea Fr., *B.*, tenera (Schaeff.) Fr., *B.*
Coprinus lagopus Fr., *S.*
Boletus granulatus (Linn.) Fr., *S.*
Polyporus squamosus (Huds.) Fr., *S.*, sulphureus (Bull.) Fr., *E.*, *H.*, Schweinitzii Fr., *S.*, betulinus (Bull.) Fr., *S.*, radiatus (Sow.) Fr., *E.*
Fomes annosus Fr., on beech, *E.*, ferruginosus (Schrad.) Mass., *H.*
Ganoderma applanatum (Pers.) Pat., *B.*
Polystictus versicolor (Linn.) Fr., *B.*, abietinus (Dicks.) Fr., *B.*
Stereum hirsutum (Willd.) Fr., *B.*, *H.*, *E.*
Corticium caeruleum (Schrad.) Fr., *S.*
Peniophora longispora (Pat.) v. Hoehn. & Litsch., *B.*
Coniophora puteana (Schum.) Karst., *B.*
Auricularia auricula-Judae (Linn.) Schroet., *S.*

GASTEROMYCETES

Phallus impudicus (Linn.) Pers., *S.*

UREDINALES

Uromyces Scillarum (Grev.) Wint., *B.*, *H.*, Valerianae (Schum.) Fuck., on *Valeriana officinalis*, *B.*, Poae Rab., on *Ranunculus Ficaria*, *B.*, Ficariae (Schum.) Lév., *B.*
Puccinia Violae (Schum.) DC., *S.*, *H.*, fusca (Pers.) Wint., *H.*, Taraxaci Plowr., *E.*, obscura Schroet., on *Luzula*, *S.*, obtegens (Link) Tul., *S.*, *B.*, Anthoxanthi Fuck., *B.*
Kuehneola albida (Kuehn.) Magn., *E.*
Melampsora Rostrupii Wagn., *B.*, *H.*, *S.*
Melampsoridium betulinum (Pers.) Kleb., *B.*
Milesia Scolopendrii Syd., *H.*

USTILAGINALES

Ustilago violacea (Pers.) Wint., *H.*
Tilletia striiformis (Westend.) Magn., *S.*
Entyloma Ranunculi (Bon.) Schroet., *B.*
Urocystis Anemones (Pers.) Schroet., *S.*

PLECTASCALES

Elaphomyces granulatus Fr., *H.*

PYRENOMYCETES

Nectria cinnabarina (Tode) Fr., *S.*, Aquifolii (Fr.) Berk., *S.*
Hypocrea pulvinata Fuck., *S.*
Rosellinia velutina Fuck., *B.*
Melanomma pulvisculum (Curr.) Sacc., *B.*
Stigmatea Robertiani Fr., *B.*
Berlesiella nigerrima (Blox.) Sacc., on *Eutypa flavovirescens*, *S.*
Leptosphaeria acuta (Moug. & Nestl.) Karst., *B.*
Valsa stellulata (Fr.) Sacc., *B.*, diatrypa Fr., *B.*
Quaternaria Persooni Tul., *B.*
Diatrypella quercina (Pers.) Nits., *S.*, verrucaeformis (Ehrh.) Nits., *S.*, Tocciaeana de Not., *B.*
Diatrype Stigma (Hoffm.) Fr., *S.*, disciformis (Hoffm.) Fr., *S.*
Ustulina vulgaris Tul., *S.*, *B.*
Hypoxylon coccineum Bull., *S.*, fuscum (Pers.) Fr., *S.*
Xylaria Hypoxylon (Linn.) Grev., *S.*, polymorpha (Pers.) Grev., *B.*

HYSTERIALES

Lophodermium Pinastri (Schrad.) Chev., *H.*

DISCOMYCETES

Dasyobolus immersus (Pers.) Sacc., on deer dung, *B.*
Lasiobolus equinus (Müll.) Karst., on deer dung, *B.*
Arachnopeziza aurelia (Pers.) Fuck., on *Quercus* cupule, *H.*
Micropodia pteridina (Karst.) Boud., *S.*
Chlorosplenium aeruginosa (Oeder) de Not., *S.*
Dasyscypha bicolor (Bull.) Fuck., *B.*, virginea (Batsch) Fuck., *B.*, fuscescens (Pers.) Rehm, *S.*
Urceolella versicolor (Desm.) Boud., on *Pteris*, *H.*
Trichopeziza escharoides (B. & Br.) Boud., *E.*
Mollisia cinerea (Batsch) Karst., *S.*, *B.*
Stegia Ilicis Fr., *H.*
Colpoma quercinum (Pers.) Wallr., *B.*

PHYCOMYCETES

Cystopus candidus (Pers.) de By., on *Cardamine*, *H.*
Plasmopara nivea (Ung.) Schroet., on *Aegopodium*, *S.*
Pilobolus crystallinus (Wigg.) Tode, on rabbit and deer dung, *B.*

PROTOMYCETACEAE

Protomyces macrosporus Ung., on *Aegopodium*, *H.*

DEUTEROMYCETES

Phyllosticta Camelliae Westend., *S.*
Septoria Ficariae Desm., *B.*, Rubi Westend., *H.*
Staganospora Curtisii (Berk.) Sacc., *S.*
Gloeosporium taxicolum Allesch., *S.*
Melanconium stilbostoma (Fr.) Tul., *B.*
Pestallozia funerea Desm., on *Rhododendron*, *S.*

Monilia aurea (Link) Gmel., on *Quercus* bark, *B.*
Oidium alphitoides Griff. & Maubl., *E.*, erysiphoides Fr., on *Myosotis*, *H.* Cyparissiae Syd., *H.*
Gliocladium penicillioides Cda., on *Comatricha typhoides*, *B.*
Ovularia primulana Karst., *B.*
Acrostalagmus cinnabarinus Cda., on *Polyporus squamosus*, *E.*
Ramularia Ranunculi Peck, *H.*, Spiraeae Peck, *S.*, *B.*, Primulae v. Thüm., *S.*, Taraxaci Karst., *E.*
Coniothecium complanatum (Nees) Sacc., on *Salix*, *B.*
Torula antennata Pers., *S.*
Cladosporium herbarum (Pers.) Link, on *Aucuba Japonica*, *S.*
Sporocybe Azaleae Peck, *B.*, *E.*
Stilbella erythrocephala (Ditm.) Lind., on deer and rabbit dung, *B.*
Stysanus stemonites Cda., *S.*

MYCETOZOA

By T. Petch

Ceratiomyxa fruticulosa Macbr., *B.*
Fuligo septica Gmel., *B.*
Diderma deplanatum Fr., *B.*
Comatricha typhoides Rost., *B.*
Reticularia Lycoperdon Bull., *S.*, *B.*
Lycogala epidendrum Fr., *B.*, *H.*, *S.*
Trichia affinis de By., *S.*, scabra Rost., *B.*, decipiens Macbr., *B.*
Hemitricha vesparium Macbr., *B.*
Arcyria denudata Wettst., *B.*

THE KILLARNEY FORAY

20–26 *September*, 1936

By J. RAMSBOTTOM

The fortieth Autumn Foray and Annual General Meeting was held at Killarney at the invitation of a number of representative Irish botanists. The headquarters was the Glebe Hotel and here most of the members assembled on Saturday, Sept. 20th. The weather had been dry for an unusual period in this notoriously moist* district beloved of the English no less than the Irish. As a consequence the number of fungi was small and several members were disappointed in not being able to attempt the correlation of the fungi to the special Pyrenean-Mediterranean type of flora and fauna.

Killarney is built in a low-lying valley of carboniferous limestone; limestone forms the promontories and islands of the Lower Lake and Muckross while the Upper Lake with its islands and surrounding woods lies well within the Old Red Sandstone. The first excursion was to Ross Island. "Ross Island itself, largely in its primitive condition in spite of planting up, is a very interesting study, with limestone ridges colonized by *Arbutus*, *Taxus*, the rare *Sorbus anglica*, *Rhamnus* spp., *Rubia*, etc.; swampy jungles with *Lastraea Thelypteris*, *Polygonum laxiflorum*, and great thickets of *Osmunda* six feet high; dry places densely occupied by *Silena maritima* and *Armeria maritima*; and rubbly stony shores with *Caltha radicans*, *Equisetum Wilsoni*, *E. trachyodon*, and so on." So writes R. L. Praeger in his *The Botanist in Ireland*; but with the scarcity of fungal growth it was not possible to decide whether any special ecological importance could be given to any species.

Lepiota excoriata, *L. gracilenta* and *L. haematosperma*, *Tricholoma resplendens*, *Cantharellus lutescens*, *Inocybe pyriodora* and *I. corydalina* figured amongst the species listed.

On Monday the excursion was to the Muckross Demesne, now the property of the Commissioners of Public works and protected as a National Park. A fair number of microfungi were found, but the larger fungi were by no means abundant. Trees of *Arbutus Unedo* were a delight to everyone—not a bush as one usually sees it along the Mediterranean, but up to thirty feet and more in height. It was cut for iron smelting in the eighteenth century and earlier, a fact which shows its abundance and is almost of itself sufficient to proclaim it a native even if records of it did not go back to the eighth century. On the fallen leaves *Septoria Unedonis* was abundant. Another plant of interest, *Euphorbia hiberna*, long used by poachers in Ireland to kill fish by placing bundles of crushed stems in streams, was found near Glena Cottage heavily infected with *Sphaerotheca tomentosa* which formed a dark brown furry cover to the stem, and also with *Melampsora Euphorbiae*. Here *Boletus scaber* var. *niveus* was found in some quantity and appearing sufficiently distinct to deserve specific rank (*B. holopus*). Several other species of *Boletus* also occurred here, notably *B. Rostkovii*; *Russula claroflava* was found in its usual damp habitat and *R. versicolor* under birches.

In the evening the Annual General Meeting was held. Mr K. St G. Cartwright was elected President and Mr F. G. Gould and Miss E. M. Wakefield, Vice-Presidents. To the general regret of members Miss Wakefield had intimated her wish to retire from the office of Secretary. A resolution was passed unanimously that Miss Wakefield should be thanked for her whole-hearted and invaluable service to the Society during her Secretaryship (1919–36) and that this should

* The annual rainfall at the Upper Lake of Killarney is 87 in.

be recorded in the minutes. The other officers were re-elected and the election of a Secretary was left open.* Messrs G. C. Ainsworth, G. J. Cooke, and P. O'Connor were elected to the Council. A report by Mr Chesters on the British Association Meeting at Blackpool was read; Dr Ainsworth was elected as the Society's delegate to the meeting at Nottingham. The nominations from the Plant Pathology committee were read and adopted.

The Deerpark and Golf Links were explored on Tuesday but with very poor results. *Lactarius volemus*, *Tricholoma grammopodium*, *Leptonia formosa*, *Marasmius esculentus* and *Geotrichum roseum* found almost immediately, suggested that there was likely to be a good list, but it petered out and *Russula versicolor* was the only species worth noting of the remaining few. In the evening Mr F. G. Gould gave his Presidential Address "The aesthetic appeal of the larger fungi".

On account of the dry conditions it was decided to go further afield the following day and Glengarriff was visited. This proved to be the best collecting ground of the foray but rain and mist interfered with members' comfort. *Pluteus pellitus*, *Cortinarius bolaris*, *Hydnum nigrum*, *Cortinarius argutus*, *Tricholoma acerbum*, *Cantharellus lutescens*, *Cortinarius tabularis*, *Ovularia destructiva*, *Cortinarius saturninus*, *Russula punctata* var. *violeipes*, *Lactarius insulsus*, *Armillaria mucida* (on oak) were amongst the more interesting finds.

A late start was made on Thursday and by very few members, because of heavy rain. Tomies Wood was visited which lies on the Lower Lake opposite Killarney. Here the boulders were a brilliant green owing to a covering of *Hymenophyllum peltatum*. The dominant tree in the area is *Quercus sessiliflora* intermixed with *Betula pubescens*, *Salix cinerea*, *Prunus spinosa*, *Corylus*, etc. It is, however, round the Upper Lake, which was not visited during the foray, that there is the largest area of native woodland now to be found in Ireland.† *Amanita muscaria* was seen here for the only time during the foray. *Leptonia formosa*, *L. lampropus* and *L. sericella* occurred in one small patch of grass along a ride; *Pleurotus ostreatus* was growing on holly. Other species were *Leptoria euchroa*, *Thecopsora Vaccinii*, *Amanita porphyria*, and *Microstroma album*.

The last excursion was to Torc. Here under holly, search was made for *Marasmius* (*Androsaceus*) *Hudsonii* and it was found in fair quantity. *Leotia lubrica*, *Russula sardonia* (*R. drimeia*), and *Macropodia macropus* were additions to the list.

Before leaving on Saturday a small party again visited Muckross. It was obvious that the rain during the week had begun to have its effect. *Lepiota amianthina*, *Gomphideus roseus*, *G. glutinosus*, *Crepidotus calolepis* (on holly) and *Monilia aurea* were additional species.

It is generally believed that in a good fungus season there would be several new records for the British Isles. Unfortunately we had not the opportunity of putting this to the test, for, on the whole, fungi were so few there was little from a mycological standpoint to repay us for the long journey. As botanists, however, we were delighted to make or renew acquaintance with many phanerogamic treasures. All present contributed to the list but I would particularly mention Mr C. Rea, Miss E. M. Wakefield, Mr A. A. Pearson and Dr P. O'Connor and also the help I received from Miss F. L. Stephens. The specimens listed as found near Festa River and Valentine's Island were collected by Mr Rea.

We are all indebted to Dr O'Connor for the arrangements he made for the foray.

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* Mr C. G. C. Chesters was elected at the November meeting.

† A description of these woods is given in E. Rübel, "The Killarney Woods." *New Phytologist*, XI (1912), 54–6. R. L. Praeger, *The Botanist in Ireland* (1934), gives much valuable information.

List of species gathered during the Foray

D. = Deerpark, *F.* = Near Festa River, *G.* = Glengarriff, *K.* = Tomies Wood, *L.* = Golf-Links, *M.* = Muckross, *R.* = Ross Island, *T.* = Torc, *V.* = Valentine's Island.

* New to British Isles.

HYMENOMYCETES

Amanita phalloides (Vahl) Fr. var. verna (Bull.) Fr., *L.*, porphyria (A. & S.) Fr., *M.*, mappa (Batsch) Fr., *G.*, *M.*, muscaria (Linn.) Fr., *K.*, spissa Fr., *G.*, rubescens (Pers.) Fr., *G.*, var. annulo-sulphurea Gillet, *G.*

Amanitopsis vaginata (Bull.) Roze, *G.*, fulva (Schaeff.) W. G. Sm., *G.*

Lepiota excoriata (Schaeff.) Fr., *R.*, gracilenta (Krombh.) Fr., *R.*, cristata (A. & S.) Fr., *M.*, castanea Quél *M.*, amianthina (Scop.) Fr., *M.*, haematosperma (Bull.) Boud., *R.*, sistrata Fr., *R.*

Armillaria mucida (Schrad.) Fr., *G.*, on oak, *R.*

Tricholoma resplendens Fr., *R.*, fulvum (DC.) Fr., *G.*, *R.*, rutilans (Schaeff.) Fr., *R.*, argyraceum (Bull.) Fr., *R.*, cuneifolium Fr., *R.*, var. griseorimosum (Batsch) Cke., *R.*, saponaceum Fr., *M.*, sulphureum (Bull.) Fr., *R.*, album (Schaeff.) Fr., *R.*, acerbum (Bull.) Fr., *G.*, *R.*, grammopodium (Bull.) Fr., *L.*, melaleucum (Pers.) Fr., *G.*, sordidum (Schum.) Fr., *L.*

Clitocybe infundibuliforme (Schaeff.) Fr., *L.*

Laccaria laccata (Scop.) B. & Br., *G.*, *M.*, *T.*, var. amethystina (Vaill.) B. & Br., *K.*

Collybia platyphylla (Pers.) Fr., *G.*, maculata (A. & S.) Fr., *L.*

Mycena avenacea (Schroet.) Fr., *M.*, elegans (Pers.) Fr., *L.*, rubro-marginata Fr., *L.*, pura (Pers.) Fr., *M.*, *R.*, *T.*, lactea (Pers.) Fr., *M.*, gypsea Fr., *M.*, galericulata (Scop.) Fr., *K.*, polygramma (Bull.) Fr., *M.*, ammoniaca Fr., *G.*, *T.*, Iris Berk., *T.*, debilis Fr., *T.*, vitilis Fr., *G.*, *M.*, *R.*, acicula (Schaeff.) Fr., *R.*, galopus (Pers.) Fr., *M.*, *T.*, tenerrima Berk., *M.*

Omphalia umbellifera (Linn.) Fr., *T.*

Russula nigricans (Bull.) Fr., *K.*, adusta (Pers.) Fr., *K.*, virescens (Schaeff.) Fr., *G.*, lepida Fr., *K.*, cyanoxantha (Schaeff.) Fr., *G.*, *M.*, *T.*, heterophylla Fr., *G.*, foetens (Pers.) Fr. *G.*, *L.*, consobrina Fr., *R.*, ochroleuca (Pers.) Fr., *L.*, *T.*, fellea Fr., *G.*, *R.*, *T.*, clavofava Grove, *G.*, drimeia Cke., *T.*, fragilis (Pers.) Fr., *T.* var. fallax (Schaeff.) Mass., *L.*, emetica (Schaeff.) Fr., *L.*, atropurpurea (Krombh.) Maire, *G.*, xerampelina (Schaeff.) Fr., *L.*, *M.*, *T.*, grisea (Pers.) Bres., *G.*, chamaeleontina Fr., *G.*, puellaris Fr., *M.*, vesca Fr., *R.*, *T.*, punctata (Gill.) Maire var. violeipes (Quél.) Maire, *G.*, caerulea Cke., *G.*, *T.*, lutea (Huds.) Fr., *G.*, *L.*, *R.*, var. armeniaca (Cke.) Rea, *L.*, Velanovskyi Melz. & Zvar. *G.*, versicolor J. Schaeff., *D.*, *M.*

Lactarius torminosus (Schaeff.) Fr., *M.*, *R.*, blennius Fr., *G.*, *L.*, uvidus Fr., *G.*, *M.*, chrysorheus Fr., *G.*, *M.*, piperatus (Scop.) Fr. *L.*, *R.*, vellereus Fr., *R.*, deliciosus (Linn.) Fr., *L.*, *R.*, pallidus (Pers.) Fr., *R.*, quietus Fr., *G.*, *M.*, fulginosus Fr., *L.*, volemus Fr., *G.*, *L.*, serifluus (DC.) Fr., *G.*, subdulcis (Pers.) Fr., *K.*

Pleurotus ostreatus (Jacq.) Fr., *K.*, mitis Berk., *K.*, limpidus Fr. *sensu* Sacc. & Bres. *M.*,* candidissimus Berk. & Curt., *K.*

Hygrophorus pratensis (Pers.) Fr., *L.*, var. cinereus Fr., *F.*, laetus (Pers.) Fr., *G.*, *M.*, *T.*, ceraceus (Wulf.) Fr., *G.*, coccineus (Schaeff.) Fr., *T.*, intermedius Pers., *F.*, conicus (Scop.) Fr., *M.*, chlorophanus Fr., *F.*, *G.*, *M.*, *T.*, psittacinus (Schaeff.) Fr., *R.*

Cantharellus cibarius Fr., *G.*, *R.*, tubaeformis Fr., *G.*, lutescens (Pers.) Fr., *R.*

Marasmius esculentus (Wulf.) Karst., *L.*, hariolorum (DC.) Quél., *L.*, dryophilus (Bull.) Karst., *M.*, *R.*, *T.*, var. aquosus (Bull.) Rea, *K.*, ramealis (Bull.) Fr., *R.*

Androsaceus rotula (Scop.) Pat., *G.*, *M.*, *R.*, androsaceus (Linn.) Pat., *K.*, Hudsonii (Pers.) Pat., *K.*, *T.*

* See p. 12.

Panus stipticus (Bull.) Fr., *G.*, *R.*, torulosus (Pers.) Fr., *L.*
Pluteus cervinus (Schaeff.) Fr., *G.*, *M.*, pellitus (Pers.) Fr., *G.*, chrysophaeus (Schaeff.) Fr., *M.*, umbrinellus (Sommerf.) Fr., *M.*
Entoloma prunuloides Fr., *F.*, jubatum Fr., *L.*, rhodopolium Fr., *M.*, nidorosum Fr., *G.*
Nolanea pascua (Pers.) Fr., *M.*, *T.*, proletaria Fr., *M.*, *T.*, mammosa (Linn.) Fr., *M.*, papillata Bres., *M.*
Leptonia lampropus Fr., *M.*, serrulata (Pers.) Fr., *M.*, *T.*, euchroa (Pers.) Fr., *M.*, sericella (Fr.) Quél., *M.*, formosa Fr., *F.*, *G.*, *M.*, *T.*, chloropolia Fr., *M.*,* Queletii Boud., *M.*
Clitopilus prunulus (Scop.) Fr., *G.*, *R.*
Claudopus variabilis (Pers.) W. G. Sm., *M.*, *R.*
Paxillus involutus (Batsch) Fr., *F.*, *R.*, *T.*
Pholiota erebia Fr., *R.*, *T.*, mutabilis (Schaeff.) Fr., *G.*
Inocybe pyriodora (Pers.) Fr., *R.*, tomentosa (Jungh.) Quél., *M.*, corydalina Quél., *R.*, geophylla (Sow.) Fr., *R.*, *T.*, obscura (Pers.) Fr., *T.*, fastigiata (Schaeff.) Fr., *M.*, *R.*
Astrosporina praetervisa (Quél.) Schroet., *M.*, lanuginosa (Bull.) Schroet., *K.*, petiginosa (Fr.) Rea, *M.*, decipientoides (Peck) Pears. *T.*
Hebeloma fastilbe Fr., *M.*, glutinosum (Lindgr.) Fr., *R.*, testaceum (Batsch) Fr., *R.*, mesophaeum Fr., *M.*, crustuliniforme (Bull.) Fr., *M.*, *R.*, var. minimus Cke., *R.*
Galera hypnorum (Schrank) Fr., *K.*, mycenopsis Fr., *R.*
Naucoria siparia Fr., *M.*, escharoides Fr., *G.*
Tubaria furfuracea (Pers.) W. G. Sm., *M.*
Flammula gummosa (Lasch) Fr., *M.*, rubicundula Rea, *G.*
Cortinarius (Phlegmacium) turmalis Fr., *G.*, balteatus Fr., *G.*, *R.*, varius (Schaeff.) Fr., *G.*, cyanopus (Secr.) Fr., *M.*, infractus (Pers.) Fr., *M.*, purpurascens Fr., *T.*, causticus Fr., *R.*, (Myxacium) elatior Fr., *G.*, *M.*, delibutus Fr., *G.*, (Inoloma) bolaris Fr., *G.*, *M.*, (Dermocybe) tabularis (Bull.) Fr., *G.*, anomalus Fr., *G.*, lepidopus Cke., *M.*, cinnamomeus (Linn.) Fr., *K.*, (Telamonia) torvus Fr., *G.*, *T.*, impennis Fr., *M.*, hinnuleus (Sow.) Fr., *M.*, brunneus (Pers.) Fr., *G.*, hemitrichus Fr., *G.*, (Hydrocybe) saturninus Fr., *G.*, castaneus (Bull.) Fr., *G.*, uraceus Fr., *G.*, *M.*, decipiens (Pers.) Fr., *R.*, acutus (Pers.) Fr., *M.*, obtusus Fr., *M.*, *T.*
Bolbitius titubans (Bull.) Fr., *M.*
Crepidotus mollis (Schaeff.) Fr., *M.*, applanatus (Pers.) Fr., *M.*, calolepis Fr., *M.*
Psaliota arvensis (Schaeff.) Fr., *G.*, sylvatica (Schaeff.) Fr., *M.*, *R.*
Stropharia aeruginosa (Curt.) Fr., *M.*, semiglobata (Batsch) Fr. *F.*, *G.*
Hypholoma fasciculare (Huds.) Fr., *K.*, *R.*, instratum Britz., *T.*, lacrymabundum Fr., *L.*, velutinum (Pers.) Fr., *R.*, hydrophilum (Bull.) Fr., *G.*
Psilocybe sarcocephala Fr., *T.*, ericaea (Pers.) Fr., *L.*, uda (Pers.) Fr. var. polytrichi Fr., *G.*, var. elongata (Pers.) Fr., *K.*, semilanceata Fr., *L.*, foenesecii (Pers.) Fr., *R.*
Anellaria separata (Linn.) Karst., *G.*
Gomphidius glutinosus (Schaeff.) Fr., *M.*, roseus (Fr.) Quél., *M.*
Psathyrella gracilis Fr., *R.*, disseminata (Pers.) Fr., *L.*, *R.*
Panaeolus sphinctrinus Fr., *F.*, *L.*, *R.*, campanulatus (Linn.) Fr., *F.*, *L.*
Coprinus sterquilinus Fr., *L.*, *R.*, plicatilis (Curt.) Fr., *R.*, *T.*
Boletus luteus (Linn.) Fr., *L.*, *M.*, *R.*, elegans (Schum.) Fr., *L.*, *M.*, *T.*, *R.*, granulatus (Linn.) Fr., *M.*, *R.*, badius Fr., *G.*, *K.*, *M.*, bovinus (Linn.) Fr., *G.*, *M.*, *R.*, *T.*, piperatus (Bull.) Fr., *K.*, *M.*, chrysenteron (Bull.) Fr., *L.*, *M.*, *R.*, subtomentosus (Linn.) Fr., *L.*, Rostkovii Fr., *M.*, versicolor Rostkv., *R.*, parasiticus (Bull.) Fr., *K.*, edulis (Bull.) Fr., *G.*, *M.*, *R.*, reticulatus (Schaeff.) Boud., *M.*, luridus (Schaeff.) Fr., *M.*, *R.*, erythropus (Pers.) Quél. *G.*, *M.*, *R.*, duriusculus Schulz., *L.*, *M.*, versipellis Fr., *R.*, scaber (Bull.) Fr., *G.*, *L.*, *M.*, *T.*, var. niveus Fr., *G.*, *L.*

* See p. 12.

Polyporus nummularis (Bull.) Quél., *R.*, varius Fr., *M.*, squamosus (Huds.) Fr., *L.*, *M.*, Boucheanus (Klotzsch) Fr., *V.*, sulphureus (Bull.) Fr., *M.*, giganteus (Pers.) Fr., *R.*, betulinus (Bull.) Fr., *M.*, *R.*, adustus (Willd.) Fr., *L.*, fragilis Fr., *G.*, caesius (Schrad.) Fr., *K.*, *M.*, *R.*
Fomes ferruginosus (Schrad.) Mass., *R.*
Ganoderma applanatum (Pers.) Pat., *R.*
Poria hymenocystis B. & Br., *K.*
Polystictus versicolor (Linn.) Fr., *G.*, *K.*, *M.*, *R.*
Daedalea biennis (Bull.) Quél., *M.*
Irpex obliquus (Schrad.) Fr., *R.*
Fistulina hepatica (Huds.) Fr., *G.*, *K.*
Hydnum repandum (Linn.) Fr., *G.*, *K.*, *L.*, *M.*, *T.*, var. rufescens (Pers.) Fr., *G.*, *L.*, nigrum Fr., *G.*, melaleucum Fr., *M.*, cyathiforme (Schaeff.) Fr., *L.*, *M.*, ferrugineum Fr., *L.*, *M.*
Mycoleptodon fimbriatum (Pers.) Boud. & Galz., *M.*, *R.*
Radulum orbiculare Fr., *R.*
Acia fuscoatra (Fr.) Pat., *R.*
Grandinia farinacea (Pers.) Boud. & Galz., *M.*, granulosa Fr., *R.*
Dictyolus muscigenus (Bull.) Quél., *K.*
Phylacteria palmata (Scop.) Pat., *R.*
Hypochnus ferrugineus (Pers.) Fr., *M.*, fuscus (Pers.) Fr., *M.*, *R.*
Stereum spadiceum Fr., *K.*, rugosum (Pers.) Fr., *R.*, hirsutum (Willd.) Fr., *G.*, *R.*, purpureum (Pers.) Fr., *M.*
Corticium porosum Berk. & Curt., *M.*, praetermissum (Karst.) Bres., *M.*
Peniophora Aegerita von Hoehn. & Litsch., *R.*, velutina (DC.) Cke., *R.*, hydnoides Cke. & Mass., *K.*, *M.*, *R.*, *T.*, cinerea (Fr.) Cke., *K.*, carneola Bres., *G.*, *M.*
Cyphella villosa (Pers.) Karst., *D.*
Solenia fasciculata Pers., *M.*
Clavaria cristata (Holmsk.) Fr., *L.*, *M.*, *T.*, rugosa (Bull.) Fr., *G.*, corniculata (Schaeff.) Fr., var. pratensis (Fr.) Cotton & Wakef., *G.*, fusiformis (Sow.) Fr., *L.*, *M.*, luteo-alba Rea, *K.*, dissipabilis Britz., *R.*
Typhula filiformis (Bull.) Fr., *M.*, gracillima White, *R.*
Pistillaria quisquiliaris Fr., *K.*
Tremella lutescens Pers., *M.*, albida (Huds.) Fr., *K.*, *M.*
Exidia nucleata (Schwein.) Rea, *R.*
Sebacina fugacissima Bourd. & Galz., *G.*, grisea (Pers.) Bres., *R.*
Calocera stricta Fr., *K.*

GASTEROMYCETES

Lycoperdon perlatum Pers., *M.*, velatum Vilt., *K.*, pyriforme (Schaeff.) Pers., *M.*, *R.*
Cyathus striatus (Huds.) Pers., *D.*
Scleroderma aurantium Pers., *G.*, *K.*, *M.*, verrucosum (Vaill.) Pers., *G.*, *M.*

UREDINALES

Uromyces Fabae (Pers.) de By., on *Vicia Cracca*, *M.*, Kabatianus Bubák, *M.*, Dactylidis Otth., *M.*, Rumicis (Schum.) Wint., *M.*
Puccinia Cirsii Lasch, *M.*, obtegens (Link) Tul., on *Cirsium arvense*, *L.*, Lapsanae (Schultz) Fuck., *M.*, Hypochaeridis Oud., *G.*, Taraxaci Plowr., *M.*, punctata Link, on *Galium saxatile*, *M.*, Menthae Pers., on *Mentha aquatica*, *R.*, annularis (Str.) Schlecht., *T.*, Vincae Cast., *M.*, Primulae (DC.) Duby, *M.*, Saniculae Grev., *G.*, *M.*, *R.*, *T.*, Conii (Str.) Fuck., *M.*, Circaeae Pers., *M.*, *R.*, *T.*, Violae (Schum.) DC., on *Viola Riviniana*, *D.*, *G.*, *M.*, *R.*, Malvacearum Mont., *K.*, Umbilici Guép., *G.*, Iridis (DC.) Wallr., on *Iris foetidissima*, *M.*, obscura Schroet., on *Luzula sylvatica*, *D.*, *L.*, *M.*, graminis Pers., *D.*, *L.*, Lolii Niels., *D.*, *M.*, Brachypodii Otth., *M.*, Aethusae Mart.
Triphragmium Ulmariae (Schum.) Link, *M.*

Phragmidium subcorticium (Schrank) Wint., *R.*, violaceum (Schultz) Wint., *K.*, *M.*, *R.*, Rubi (Pers.) Wint., *M.*
Kuehneola albida (Kuehn) Magn., *G.*
Coleosporium Senecionis (Pers.) Fr., *K.*, *M.*, Tussilaginis (Pers.) Kleb., *M.*, Euphrasiae (Schum.) Wint., *M.*, Melampyri Tul., *G.*
Melampsora Euphorbiae (Lév.) Cast., on *Euphorbia hiberna*, *G.*, *M.*, Hypericorum (DC.) Schroet., on *Hypericum Androsaemum*, *M.*, *R.*
Melampsoridium betulinum (Pers.) Kleb., *G.*, *R.*
Pucciniastrum Circaeae (Schum.) Schroet., *R.*, *T.*
Thecopsora Vacciniorum (Link) Karst., *M.*, *T.*
Milesia Polypodii B. White., *G.*, Scolopendrii (Fuck.) Arth., *M.*, *T.*, Blechni (Syd.) Arth., *G.*, *M.*, *T.*
Aecidium pseudo-columnare Kuehn, on *Abies pectinata*, *M.*

USTILAGINALES

Ustilago Scabiosae (Sow.) Wint., *M.*
Sphacelotheca Hydropiperis (Schum.) de By., *F.*, *R.*
Entyloma microsporum (Ung.) Schroet., *D.*
Urocystis Violae (Sow.) Fisch., *M.*

PYRENOMYCETES

Sphaerotheca pannosa (Wallr.) Lév., *M.*,* tomentosa Otth., on *Euphorbia hiberna*, *M.*
Erysiphe Polygoni DC., *M.*, Cichoracearum DC., *M.*, Umbelliferarum (Lév.) de By., on *Aegopodium Podagraria*, *M.*, on *Heracleum Sphondylium*, *R.*, graminis DC., *D.*
Microsphaera Grossulariae (Wallr.) Lév., *K.*, Alni (DC.) Wint., *M.*
Uncinula Aceris (DC.) Sacc., *D.*, *R.*
Phyllactinia Corylea (Pers.) Karst., on *Betula alba*, *R.*
Irene* calostroma (Desm.) v. Hoehn., on *Rubus Idaeus*, *M.*
Nectria coccinea (Pers.) Fr., *M.*
Epichloe typhina (Pers.) Tul., on *Holcus*, *M.*
Claviceps microcephala (Wallr.) Tul., *D.*, purpurea (Fr.) Tul., on *Dactylis*, *Lolium* and *Agrostis tenuis*, *D.*
Lasiosphaeria hirsuta (Fr.) Ces. & de Not., *M.*, spermoides (Hoffm.) Ces. & de Not., *M.*
Stigmatea Robertiani Fr., *K.*, *M.*
Mycosphaerella depazaeformis (Awd.) Lind, on *Oxalis acetosella*, *G.*, *T.*, Clymenia (Sacc.) Johans. & Magn., *T.*, Idaeina (Hazsl.), *M.*, peregrina (Cke.), *M.*
Venturia Rumicis (Desm.) Wint., *K.*, inaequalis (Cke.) Wint., emend. Aderh., *M.*
Anthostomella appendiculosa (B. & Br.) Sacc., *M.*
Hypoxylon multiforme Fr., *K.*
Xylaria Hypoxylon (Linn.) Grev., *D.*, carpophila (Pers.) Fr., *K.*
Phyllachora graminis (Pers.) Fuck., *M.*, Trifolii (Pers.) Fuck., *M.*
Rhopographus Pteridis (Sow.) Wint., *D.*

DISCOMYCETES

Leptopodia elastica (Bull.) Boud., *D.*
Macropodium macropus (Pers.) Fuck., *K.*, *T.*
Taphrina Tosquineti (Westend.) Magn., on *Alnus rotundifolia*, *M.*, *R.*, Quercus (Cke.) Sacc., on *Quercus Robur*, *M.*
Exoascus Pruni Fuck., *M.*, Alni-incanae (Kuehn) P. Magn., on *Alnus rotundifolia*, *M.*
Leotia lubrica (Scop.) Pers., *M.*, *T.*
Cudoniella acicularis (Bull.) Schroet., *D.*
Calycella citrina (Hedw.) Quél., *M.*
Coryne sarcoides (Jacq.) Tul., *K.*
Bulgaria inquinans (Pers.) Fr., *G.*
Orbilia xanthostigma Fr., *K.*
Sclerotinia Curreyana (Berk.) Karst., on *Juncus conglomeratus*, *M.* (*Sclerotium*).

* New record.

Phialea firma (Pers.) Gill., *K.*
Chlorosplenium aeruginosum (Oeder) de Not., *K.*
Mollisia cinerea (Batsch) Karst., *G.*
Pseudopeziza Trifolii (Biv.-Bern.) Fuck., *M.*
Fabraea Ranunculi (Fr.) Karst., *D.*
Stegia Ilicis Fr., *G.*, *M.*
Rhytisma acerinum (Pers.) Fr., *M.*, *V.*, salicinum (Pers.) Fr., *M.*

HYSTERIALES

Lophodermium hysterioides (Pers.) Sacc., *M.*, pinastri (Schrad.) Chev., *M.*
Sporomega cladophila (Lév.) Duby, on *Vaccinium*, *M.*

PROTOMYCETACEAE

Protomyces macrosporus Ung., on *Aegopodium Podagraria*, *M.*

PHYCOMYCETES

Cystopus candidus (Pers.) de By., on *Cardamine hirsuta*, *D.*
Plasmopara nivea (Ung.) Schroet., on *Aegopodium Podagraria*, *M.*
Bremia Lactucae Regel, on *Senecio vulgaris*, *D.*, on *S. Jacobaea*, *M.*
Peronospora alta Fuck., on *Plantago major*, *D.*, parasitica (Pers) Tul., on *Sisymbrium*, *M.*

DEUTEROMYCETES

Phyllosticta Dulcamarae Sacc., *D.*
Actinonema Rosae (Lib.) Fr., *M.*
Septoria Rubi Westend., *M.*, Unedonis Rob. & Desm., *M.*, Brissaaceana Sacc. & Let., *M.*, Dianthi Desm., on *Dianthus barbatus*, *R.*, Rubiae (Pat.) Bub. & Ranoj., on *Rubia peregrina*, *M.*, Violae Westend., *D.*, *G.*, Podagrariae Lasch, *M.*, exotica Speg., *G.*, Convolvuli Desm., on *Calystegia sepia*, *D.*, *M.*, Senecionis-sylvatici Syd., *L.*, scabiosicola Desm., on *Scabiosa succisa*, *D.*, *T.*
Microstroma album (Desm.) Sacc., K.
Monilia aurea (Pers.) Gmel., *M.*
Geotrichum roseum Grove, on various grasses, *D.*
Oidium alphitoides Griff. & Maubl., *G.*, *M.*, *T.*, Evonymi-japonicae (Arcang.) Sacc., *M.*
Trichoderma viride Fr., *T.*
Rhinotrichum Thwaitsii B. & Br., *D.*, *G.*
Sepedonium chrysospermum (Bull.) Fr., *D.*
Ovularia destructiva (Phill. & Plowr.) Mass., *G. K.*, Veronicae (Fuck.) Sacc., on *Veronica chamaedrys*, *T.*, primulana Karst., *M.*, obliqua (Cke.) Oud., on *Rumex obtusifolius*, *D.*, *M.*
Botrytis cinerea Pers., on *Scilla non-scripta*, *D.*
Didymaria didyma Schroet., on *Ranunculus repens*, *R.*
Mastigosporium album Riess var. muticum Sacc. on *Dactylis*, *L.*
Ramularia Circaeae Allesch., *M.*, Sambucina Sacc., *D.*, arvensis Sacc., on *Potentilla*, *G.*, Spiraeae Peck, *M.*, Taraxaci Karst., *M.*, Lampsanae (Desm.) Sacc., *M.*, calcea (Desm.) Ces., *R.*, *T.*, filaris Fres., var. lappae Bres., on *Arctium minus*, *M.*, variabilis Fuck., on *Digitalis*, *D.*, *G.*, Parietariae Pass., *R.*, Urticae Ces., *D.*, Rhei Allesch., on *Rheum officinale*, *R.*, Hypochaeridis P. Magn. *G.*, Scrophulariae Fautr. & Roum., *M.*, lychnicola Cke., *M.*, Kriegeriana Bres., *M.*
Bispora monilioides Cda., *G.*
Cladosporium herbarum (Pers.) Link, *M.*, Graminum Cda., on *Phalaris arundinacea*, *M.*
Polythrincium Trifolii Kze., *T.*
Heterosporium Magnusianum Jaap, on *Narthecium ossifragum*, *M.*
Cercospora Apii Fres., *G.*, Lythri (Westend.) Niessl, *G.*, lilacina Bres., on *Viola.*, *T.*
Macrosporium sarcinaeforme Cav., on *Trifolium pratense*, *M.*
Sporocybe Azaleae Peck, on *Rhododendron*, *G.*
Sclerotium roseum Moug. & Nestl., *M.*

NOTES ON KILLARNEY AGARICS

By A. A. PEARSON

LEPTONIA QUELETII Boudier, *Icones Mycol.* Pl. 100.

Pileus 1–3 cm., convex, depressed in centre, submembranaceous but fairly firm, incurved at first, delicate violaceous pink, deeper in centre, pale round margin or fawn colour without trace of pink; minutely squamulose with a delicate sheen, flesh white, pink under cuticle. *Gills* subdistant, emarginate with a decurrent tooth, fairly broad, 2–3 mm., linear or ventricose, white then pink, edge straight or undulate. *Stem* 4–6 cm. long, about 2 mm. thick, firm, hollow, white, minutely fibrillose, with white tomentose base. *Basidia* 4-spored. *Spores* in mass pink, nodulose, mostly with blunt angles and sharply pointed apiculus, 9–11 × 6·7 μ. *Cystidia* none; cuticle of pileus of elongate hyphae 8–10 μ. wide, septate, hyaline, mixed with patches of coloured hyphae which give the pink tinge to the pileus. *Taste* mild. No smell.

Habitat: in troops among grass and moss under trees.

National Park, Muckross Demesne, Killarney, Ireland, 21 September 1936.

Arthog, Merionethshire, Wales, 19 September 1937. Mr G. J. Cooke.

PLEUROTUS CANDIDISSIMUS Berk. & Curtis in *Ann. Mag. Nat. Hist.* (1859).

Pileus 0·5–1 cm., pure white, membranous, shell-like, finely pulverulent, slightly undulate, edge incurved. *Gills* white, crowded, thin. *Stem* rudimentary, the base of receptacle sometimes more or less elongated. *Spores* globose, 5–6 μ, apiculate, smooth, hyaline, with granular contents or 1-guttulate.

Killarney, 24 September 1936.

Specimens were brought in at the meeting of the British Mycological Society, and the above notes made by me. I was able to trace the species in the monograph of *Pleurotus* by Dr Albert Pilát (Prague, 1935). It closely resembles *P. septicus* and *P. chioneus* from which it differs in the globose spores. As these small Pleuroti are often passed over, it may not be uncommon.

MYCETOZOA FOUND DURING THE KILLARNEY FORAY

20–26 *September*, 1936

By G. LISTER.

Our party was favoured with fine mild weather on most days. The beautiful woods around the lakes consisted of oak, ash, birch, holly, arbutus, hazel, scots pine and spruce, with undergrowth of bramble, ivy, heather and bilberry. Fallen wood was fairly plentiful, yet, as found in other parts of Ireland, Mycetozoa were not abundant. The moist climate induces a rapid growth of moss on fallen logs, and hosts of woodlice and small snails feed on immature sporangia, and these conditions may account to some extent for the scanty harvest of species obtained. Amongst the eighteen species recorded were three new to Munster, viz. *Didymium melanospermum* (Pers.) Macbr. var. *minus* Lister, *Licea pusilla* Schrad., and *Trichia floriformis* (Schw.) Lister: the last formed a colony several inches long on a rotten fir log: another species, *Cribraria violacea* Rex, is a new record for Ireland; eight minute purple sporangia were found on a birch stick, nestling among a brown mould.

In the following list *R.* stands for Ross Castle which we visited on 20 September; *M.* for Muckross Abbey and Dinnes Island; *DP.* for Deer Park; *G.* for Glengarriff; *T.* for Tomies Mountain; *K.* for Kenmare Demesne; *TW.* for Torc Waterfall, to which places we made excursions on the succeeding days.

Ceratiomyxa fruticulosa (Muell.) Macbr., *M.*
Physarum nutans Pers., *R.*, *G.*, *T.*; virescens Ditm. var. nitens Lister, *G.*
Fuligo septica (L.) Gmel., *M.*, *DP.*, *G.*, *T.*, *TW.*
Didymium melanospermum (Pers.) Macbr. var. minus Lister, *G.*
Stemonitis fusca Roth., *R.*, *M.*, var. rufescens Lister, *R.*; splendens Rost. var. Webberi Rex, *G.*
Comatricha nigra (Pers.) Schroet., *M.*, *K.*; typhoides (Bull.) Rost., *T.*
Cribraria violacea Rex, *M.*
Licea pusilla Pers., *TW.*
Lycogala epidendrum (L.) Fr.
Trichia persimilis Karst., *R.*; decipiens (Pers.) Macbr., *R.*, *DP.*; floriformis (Schw.) Lister, *TW.*
Arcyria denudata (L.) Wettst., *R.*, *M.*; incarnata Pers., *T.*; cinerea (Bull.) Pers., *R.*

PRESIDENTIAL ADDRESS

THE AESTHETIC APPEAL OF THE LARGER FUNGI

By F. G. GOULD

The British Mycological Society was established at Selby in 1896, and at the outset it was very largely concerned with the study and appreciation of the larger fungi met with in the field and popularly known as toadstools. In more recent years, however, the membership has been increasingly concerned with fungi in their relation to plants of economic importance. This has involved careful detailed study of groups which are detected mainly by irregular appearances on their hosts. The structure of the various species can only be seen by using a microscope. They seldom have any aesthetic attraction for the naked eye. More often they induce repulsion as the cultivator recognizes diseases which he knows will reduce the value of his crops or destroy them.

Modern mycology has become to a large extent the study of plant pathology, and it must be admitted that the development of this vitally important subject is now one of the principal reasons for the prosperity of our Society. We embody to a large extent the research staffs of agricultural and horticultural institutions the world over.

Then there is a considerable section of our membership, often working hand in glove with the plant pathologists, whose vocation it is to study life histories of fungi, to ascertain in the greatest possible detail the way in which any given fungus grows, and the exact stages through which it passes from its beginning to its end. Much of this work is pure scientific research, undertaken for the love of knowledge for its own sake and not necessarily related to means of preventing disease in plants of economic importance.

There is a third section of our membership drawn from the tutorial staffs of various educational establishments. These members give instruction to students from whom the research workers and plant pathologists of the future may be recruited, and many of them are themselves engaged actively in research. These teachers, especially in the London area, find the forays held by our Society of great use in supplementing their own teaching and in stimulating students to take an interest in field work. Closely associated in function with the teachers are the curators and staffs of museums, from whose ranks come some of the most active of our members.

Probably most of us who belong to one of these categories are professionally engaged in mycology. Of the original fifty foundation members about 70 per cent appear to have been amateurs: but of the three hundred present-day individual members, as distinct from some sixty corporate bodies which are enrolled as members, only about 24 per cent appear to be amateurs and of these about one-third attend more or less regularly our spring and autumn forays. Even from this small number must be deducted several members whose main interest is in the Mycetozoa and lichens.

Your President for 1936 has been drawn from this small and possibly dwindling body of amateurs who interest themselves in mycology either as a major hobby or as a more or less seasonal interest among all the other attractions of plant life. The members who belong to it are in the main botanical students in the limited sense; that is, people who enjoy training their powers of observation so that they can recognize and give a name to all species of plants they encounter in the field. They have been led to study fungi for much the same reason as they were led to study phanerogams and the other divisions of the cryptogams. They get pleasure from the power to recognize distinct species and varieties. Perhaps I may be allowed to say that I was led to a study of the larger fungi by listening to a lecture on toadstools in the autumn of 1902, included in a University Extension Course on Nature Study delivered at Toynbee Hall in East London. I doubt if at that time the lecturer had more than a simple text-book knowledge of the subject. She had obtained a basket of toadstools collected haphazard, and drew from this to describe the principal types as far as the contents would allow. They must have been good specimens, for from that day I have not ceased to devote time every autumn to the search for kinds hitherto unfamiliar, and to the renewal of acquaintance with species met with in the past, but unfortunately often quickly forgotten. My interest was stimulated a few weeks later by the chance discovery in a second-hand bookshop of a copy of *British Edible Fungi*, by M. C. Cooke. This contains many beautiful illustrations which made a great impression on me. I was a town-dweller whose excursions into the country were limited in the main to my annual summer holiday, and the plants of the wayside appeared to me then as a mass of vegetation rather than as an assembly of different individuals. I had hardly realized the existence of toadstools, and had passed over with indifference the occasional appearance of small specimens on the lawn of my father's garden. The Toynbee Hall lecture and Cooke's book sent me off to Epping Forest where I expected to find resplendent toadstools sprouting from every tree and clothing the ground with their dainty colourful forms. Needless to say I was disappointed. That fruitless journey on a cold November afternoon was not dissimilar in result from many a day spent since

with the British Mycological Society in various English woodlands, when fungi of interest to me at any rate have been conspicuous by their absence. Cooke's brightly illustrated books continued, however, to interest me. I discovered his "Plain and easy account of British Fungi" with its alluring coloured pictures of *Clathrus cancellatus*, *Amanita muscaria* and certain of the Russulas. Then I found a simple *Fungus-Hunter's Guide*, by W. Delisle Hay, which by means of artificial keys assists the student to determine the genera and species of the fungus under notice. Not till 1911 did I acquire a copy of George Massee's *British Fungi and Lichens* with its forty beautiful coloured plates illustrating some two hundred out of the twelve hundred species more or less briefly described.

On 15 October 1904 I took part in the Saturday Fungus Foray in Epping Forest of the Essex Field Club, and with two exceptions, when illness prevented me, I have attended this annual meeting ever since. On the first occasion I met Dr M. C. Cooke, then in his eightieth year; this turned out to be the last at which he assisted, although he did not die until ten years later. I had the satisfaction of getting him to name for me a specimen, *Clitocybe gilva*, which only once have I seen since. If I could produce a descendant of this specimen now it would probably be given another name.

The Essex Field Club brought me into touch with prominent members of the British Mycological Society, in particular Miss Elsie Wakefield, Miss G. Lister, Miss Lorrain Smith, Mr A. A. Pearson and Mr J. Ramsbottom, for whose patient help and kindly consideration over a long period of years I express my gratitude.

Membership of the British Mycological Society followed in 1918 and with it access to the fund of knowledge possessed by Mr Carleton Rea, whose book, *British Basidiomycetae*, published in 1922, has since been my principal literary standby.

It will be gathered from these personal notes that it was the aesthetic appeal of the toadstool which attracted me, and it is with this aspect that I want to deal. Beauty appeals to us through form, colour and smell. It is enhanced by the setting of the object. But once interest is aroused by the beauty of a particular species, *Lactarius aurantiacus* for example, we are led to examine closely all other species of the genus we encounter. We take pleasure in noticing the distinguishing features and come ultimately to be interested in such a relatively loathsome object as *L. turpis*.

The first toadstool I succeeded in getting named correctly was *Lepiota procera*. It appeared in my father's garden in North London. I bore it in triumph to the lady at Toynbee Hall who first awakened my interest, but she, alas! looked at it with an expression of deprecating wonderment. George Massee came to my rescue. Although all Lepiotas attract me, *L. procera* does so most of all. It has grace of

outline and delicacy of colour. I admire the large cap with its scales and prominent dark umbo, its relatively long, slender stem with snake-like markings, its movable ring and its bulbous base. I have sampled its edible qualities and found them good. It is said to be common and no doubt it is, but I have never found it often enough to feel tired of seeing it. We met it abundantly in Windsor Park in 1923, but only occasionally at other forays since. A feature of our meeting at Haslemere in 1932 was *L. clypeolaria*, found in woods at Cocking on the South Downs. It is a delicate fungus, easily damaged in the gathering, and not to be trusted with those mycologists who cannot refrain from handling toadstools as if they were dumbbells. Its special feature is the dense yellow or brownish felt which at first covers the cap and then breaks up into torn woolly patches. *L. felina* is another handsome little fellow with its blackish concentric scales on the cap. Most pleasing, too, is the white *L. cristata* which sometimes appears on lawns, and the small, rich, yellow *L. granulosa* and *L. amianthina* occurring in woods, sometimes on moss.

The genus *Psaliota* includes many species of beauty, although I have not been fortunate enough to see many. One of the handsomest, which occurred abundantly near Totnes last year was the variety *lepiotoides* of *Psaliota xanthoderma*. The name suggests that it resembles a *Lepiota*, but of course it has purple spores.

Anellaria separata, with its tense, straight, rigid, ringed stem surmounted by its large bell-shaped cap, is in fact a handsome object, but as it is usually found on generous heaps of horse manure it does not make a picture, except perhaps to the horticulturist.

Now I pass on to *Amanitopsis vaginata*, surely among the most graceful and delicate as well as the most common of fungi. The cap expanding from the shape of half an egg to a flat disk three or four inches across is white, grey or bright brown and bears patches of the sheath, the rest of which remains in the ground through which it burst. The delicate striations of the margin are a pleasing feature. The fungus is of delicate texture and great care has to be exercised to gather it complete with its volva. I have seen it of large size in great quantities in the woods near Llangollen, but small specimens may always be met with in the autumn.

An allied genus of some beauty, with pink spores, is *Volvaria*. I once found *V. volvacea* in my garden at Loughton, and *V. bombycina* occurred in quantity on a decaying elm stump close by. It is a large fungus with a yellowish silky cap, long stem and ample white volva, a really handsome object and bound to give pleasure to any naturalist who is lucky enough to find it.

The genus *Amanita* contains many beautiful species, first and foremost among them being the brilliant scarlet *A. muscaria*. To see troops of these in open birch glades spangling the yellow carpet of falling

leaves is to experience pleasure which does not dull with frequent repetition. The intense colour of the cuticle of the pileus is heightened by contrast with the yellowish fragments of the volva with which it is studded, and with the bold, white, ring-encircled stem. No wonder that it has attracted much attention and that certain more or less useful qualities have been discovered. As long ago as 1847, Mrs T. J. Hussey wrote: "An extract from it has been recommended in doses of from 10 to 30 grains for epilepsy and externally as a dressing for ulcers. The expressed juice is said to purify furniture from noxious insects. The Coreans of Kamschatka use it in decoction for their drinking festivities. It produces delirious intoxication and under its influence Tartars are supposed to be divinely inspired and to speak oracles."

Almost as attractive to look at, although more subtle and elusive and still less respectable, is *A. phalloides*. The aesthetic attraction to me is the large greenish or yellowish olive cap streaked with dark innate fibrils. The occasional fragments of the volva throw up this colour, and it contrasts well with the long white stem and well-formed ring. A description of the extremely dangerous qualities of this fungus is outside the scope of this paper, and for those who wish to die a horrible death I can but refer them to the lurid details of the facilities provided by this fungus as described by our General Secretary in his paper entitled "Edible and Poisonous Fungi" read to the Royal Society of Medicine in 1925.

Many other species of *Amanita* are attractive, especially *A. rubescens* with its roseate tinting and robust structure.

I pass to the genus *Armillaria* to consider the two well-known species *A. mellea* and *A. mucida*. *A. mellea*, from the foresters' point of view, must be written down a nuisance, but the artist sees in it nothing but delight. It occurs around old stumps, frequently in dense masses of ochraceous yellow caps covered with brownish hairy squamules. In its early stages the young pilei crowded together like a mass of small eggs are not readily identifiable with the large groups they develop into, which sometimes cover two or three square feet. The spores dust the ground and cover the lower caps. Sometimes on a still, warm day they can be seen escaping in dense clouds. Very different is its relative *A. mucida* which is seen at its whitest and daintiest sprouting at intervals up the whole length of a dead beech. This is one of the best subjects for the photographer who desires an arresting picture.

Similar in habitat and development to *A. mellea* is *Pholiota squarrosa*, but its aesthetic effect is heightened by the rich yellow of the crowded caps and the prettily marked stems variously lengthened to bring each competing cap out from its crevice to shed its spores as far as possible. The larger *P. spectabilis* occurring in tawny groups on dead stumps is also an attractive sight in the autumn woodland.

Another toadstool which pleases me very much is *Stropharia*

aeruginosa. This has great beauty of form and colour. The cap is a verdigris green dotted with fugacious squamules. There is a delicate white ring and a graceful stem covered below the ring with white squamules.

Stropharia leads on to the great genus *Cortinarius* with its six subdivisions, every one of which contains species of beauty. Some are frequently met with, but many of the more attractive have to be searched for far and wide. The Cortinarii occur in greatest variety in coniferous woodland, and the deepest impression on my mind left by this Society's visit to the Scottish Highlands in 1927 is a picture of many Cortinarii hitherto unknown to me. Some of them are remarkable for the lovely colours of the caps, but grace of form and the elegant characters of the stem are marked features. I fear that only those among you who have some knowledge of the Cortinarii can expect to sympathize with these remarks, so I will content myself with mentioning a few species which to me are of outstanding aesthetic appeal. There is *C.* (*Phlegmacium*) *multiformis* with its cap and stem of even tawny yellow and its bulbous base—a toadstool of remarkable geometrical form; *C.* (*Myxacium*) *elatior*, the toadstool with viscid brown cap and long lilac or violet stem tapering to the base, found in quantity in beech woods; *C.* (*Inoloma*) *bolaris* with its delightful reddish cap sprinkled with darker scales; *C.* (*Inoloma*) *pholideus* with cap and stem delicately figured with blackish scales. Then come the Dermocybes which include *Cortinarius semisanguineus*, *C. cinnabarinus* and *C. sanguineus*, conspicuous in varying degrees for their deep red coloration. The Telamonias which follow are remarkable for their attractive stem markings—*C. torvus* with its bulbous stem and persistent ring, *C. armillatus* with its vermilion spirals, aptly described as the bracelet fungus; *C. hemitrichus*, *C. rigidus* and *C. paleaceus*—the despair of the careless—with their dainty conical caps, elusive rings and stem spirals. Last come the Hydrocybes, which include many beautiful forms among which I will content myself with mentioning *C. castaneus* and *C. dolobratus*.

The genus *Inocybe*, which I must now remark upon, includes a large number of species, usually small and difficult to identify. Two which are outstanding for size, namely, *I. pyriodora* and *I. incarnata* are attractive on account of their pleasant smell suggesting pears. *I. rimosa* is a species, or perhaps a group of species, which appeals to me as most elegant in form and delicate of colour. The yellowish, geometrically umbonate cap is broken up by regular cracks exposing a paler colour underneath. Then there are the white and lilac forms of *I. geophylla* which delight the eye in dark woods with their dainty little caps; *I. hystrix* is remarkable for the small porcupine-like scales which bristle on the dull brown pileus.

I now pass to the great genus *Tricholoma* which introduces the multitude of toadstools destitute of obvious ring or volva. This genus

has white spores, and it is closely associated in form with *Entoloma*, *Hebeloma* and *Hypholoma*, which are distinguished respectively by pink, yellowish and purplish black spores. They include many beautiful species. First and foremost in my eye is *Tricholoma rutilans*, often large, with the pileus covered with reddish velvety down on a yellow base, gills bright yellow and stipe a lighter yellow besprinkled with purplish squamules—a really handsome object. But the genus includes many equally attractive species; slightly outstanding perhaps are *T. sulphureum*, wholly sulphur yellow, *T. nudum* (well known as Blewits), entirely violet purple, sweet-smelling and edible; *T. melaleucum*, with nearly black umbonate cap daintily poised on a straight white stem, *T. militaris*, imposing, with a large reddish cap reminiscent of the days when soldiers wore red coats; *T. vaccinum* and *T. imbricatum*, remarkable for the tile-like scales which decorate their caps—these are but a few among many handsome species in a handsome genus.

Among the species of *Entoloma* I am always pleased to meet *E. porphyrophaeum*, sometimes abundant in pastures. The trouble of writing an address of this character is the impossibility of sufficiently differentiating descriptions to give individuality to each toadstool under notice, and I am bound to assume some sympathetic knowledge on the part of my audience. Even were I able to illustrate my remarks with coloured or plain pictures the difficulty would not be greatly removed. The colour of many toadstools is fleeting, and the strong tints fixed in the mind by an artist who has depicted his subject at its brightest are often deceptive. I enjoy *E. porphyrophaeum* because of its campanulate striate umbonate cap and tall rigid stem. Perhaps it has a mousey colour, but all I can say in defence is that I like that sort of mousey colour. The genus provided me with the most impressive picture left on my mind by our meeting in South Devon in 1935. The hillside near Berry Pomeroy Castle was studded with the white caps of *E. rhodopolium* silkily shining over rosy gills, smelling like new meal, and a constant reward for the labour of working on a steep, boulder-strewn slope.

I have never been able to work up any enthusiasm for the genus *Hebeloma*, but *Hypholoma* claims the attention of the artist with the ubiquitous *H. fasciculare*, the sulphur tuft, which sometimes cheers the mycologist despondent with unsuccessful searching, by its clump of little yellow caps emerging from the hollow of an ancient stump. The sulphur tuft has many relatives of charm, such as the tawny brick red *H. sublateritium* and the less common, ash-coloured *H. leucotephrum*. Others, with a distinct charm of their own, are *Hypholoma velutinum*, velvety as its name implies, and *H. pyrotrichum*, with a fiery tawny cap densely clothed with tawny scales.

The white-spored genus *Clitocybe* with its normally decurrent gills provides several forms which are attractive with their cup-shaped

caps. *C. infundibuliformis* is a pleasing example, while *C. clavipes* affords the contrast of an almost obconical cap surmounting a conical stem. *C. aurantiaca*, the false chanterelle, is conspicuous with its soft orange-coloured undulating cap, and is often met with on boggy heaths and in coniferous woods where it shows up gloriously among dark pine needles. The little greenish *C. odora* has the pleasant smell and taste of aniseed. The closely allied genus *Laccaria* includes *L. laccata* var. *amethystina* of a beautiful deep violet which excites the admiration even of the more prosaic.

Hygrophorus, which follows, possibly includes more lovely colour forms than any other genus. All these toadstools are fleshy, somewhat wax-like, with decurrent gills, central stems and white spores. Most of the species occur in meadows and open places, although the white *H. eburneus* and *H. cossus* are found in woods. The commonest and the more colourful are *H. pratensis*, tawny yellow with gills of the same colour, very thick, distant and decurrent; *H. laetus*, tawny, viscid and shining; *H. coccineus*, bright scarlet, sometimes large, and when seen at its best, lighting up luscious meadows as with brilliant ruby jewels; *H. miniatus*, a diminutive counterpart; *H. puniceus*, of the colour of blood; *H. calyptraeformis*, a pink form with its pileus acutely conical and curiously lobed; and *H. psittacinus*, green, yellow, purple and black, reminding one, as its name implies, of a richly plumaged parrot. These are but a few members of a most attractive genus.

I cannot overlook the pink-spored *Clitopilus prunulus*, because I never fail to enjoy the irregularly shaped whitish cap, pressed closely to the ground and smelling of new meal. Perhaps some of us do not know what new meal smells like, but we all know the pleasant aroma of which this humble little fungus gives a good example. I am content to call it the smell of *C. prunulus*, and to declare that it is good.

I am tempted to say something about every genus in the flora, as there is seldom one which is without aesthetic merit, but I must pass over brown *Flammula* and the queer, viscid *Gomphidius*, and turn for a few minutes to *Collybia*. At a normal fungus foray in the autumn, the exhibition tables are certain to be well furnished with quantities of the large white *C. maculata*, occasionally bearing reddish spots on the cap and provided with long, white, variously swollen stems. These toadstools look more pleasing growing in the woods than lying about in various unnatural attitudes on the tables. *C. radicata*, with its very long stem, swollen in the middle, tapering down into rotten wood, and carrying aloft its viscid, oblong, whitish cap, cannot be passed by with indifference even if it is too common to gather. *C. fusipes*, in clusters at the foot of oak trees, often strangely contorted but usually keeping its colour of rich mahogany, has a rugged beauty of its own, while yellow *C. velutipes*, bursting in companies from fallen timber, is an interesting feature of a walk in winter.

There is a series of genera hereabouts such as *Leptonia*, *Naucoria*, *Psilocybe*, *Panaeolus*, *Nolanea*, *Galera*, *Omphalia*, *Eccilia* and *Tubaria*, all with small species. They are nearly all charming, but I do not know them well enough to venture on any detailed remarks. I will make an exception with *Mycena*, which is usually well represented at our field meetings and contains many species of dainty beauty. Some are extremely small, for example, *M. rosella*, whose rosy cap 10 mm. across, appears on pine needles, but *M. pura*, rosy lilac and prettily campanulate, comes out in large numbers from decaying leaves. *M. polygramma*, striate of cap and dark of hue, is a pleasure to see; *M. epipterygia*, with its yellowish membranaceous cap and long, yellow, sticky stem, cannot be overlooked, while lovely little pink-belled *M. Adonis* is a great favourite with the ladies.

Among small toadstools perhaps one of the most remarkable is *Psathyrella disseminata*. The caps of individuals seldom exceed 1 cm. in diameter, but it is not unusual to see most of an old stump covered by myriads of these small, delicately striated, greyish white caps, and the mass makes a picture in the woodlands not easy to forget.

I must say a word or two about *Pleurotus*. Most of the species have excentric stipes and they are usually found extruded from the trunks of trees. Their inferential connexion with the death or approaching demise of a noble tree detracts from the pleasure given by their elegant form, but *P. ostreatus* and its varieties are not, in my experience, so obviously associated with recent or impending death. *P. ostreatus* occurs in great masses on old stumps; its variety *columbinus* has numerous dark bluish grey pilei, and it is an arresting sight when seen in perfection.

I now pass to the intensely interesting genus *Russula*. Collectively the species are easy to refer to *Russula*, but the identification of the species themselves is difficult. Practically all grow on the ground; they are compact, and regular in form; the stalks are short, the caps normally circular and often brightly coloured. There is a waxy brittleness of texture that appeals to the sense of touch. My children, when young, seldom erred in recognizing a *Russula*. The species rarely possess a strong smell, some of them are extremely acrid to the taste, and they are of little value in the kitchen. Their aesthetic attraction is the neatness of form and brightness of colour. The colour range is almost complete. *R. emetica* with its bright rosy caps generously decorates the ground in mixed woods. The deep blood-red to black of *R. atropurpurea* looks well in grassy glades; *R. ochroleuca*, *R. fellea* and *R. lutea*, not to mention less common species, delight the eye and tease the mind with their varying shades of yellow. *R. cyanoxantha*, *R. furcata* and *R. virescens* give us mixtures of green and blue. Even the relatively repulsive *R. nigricans* provides the possibility of a thrill by supporting in its old age the delicate little agaric *Nyctalis parasitica*.

Close to *Russula* comes *Lactarius*—surely the best known of all the genera of toadstools, because of the abundance of some of the species and their very convenient feature of exuding, when bruised, what is usually a milk-like fluid. Many of them, such as *L. quietus* and *L. cimicarius*, are apt to repel by their oily and sometimes verminous odour, but *L. glyciosmus* (the name means "sweet scent"), provides an aromatic contrast. Some, such as *L. pyrogalus*, *L. rufus* and *L. piperatus* rival the worst of the Russulas in acridity; but others, such as *Lactarius volemus* and *L. deliciosus* are reputed worthy of the gourmet's table. Bright and delicate colours are to be met with. *L. torminosus* and *L. pubescens*, comely in shape, have shades of flesh and strawberry streaked silkily with white; *L. aurantiacus*, bright golden orange, *L. rufus*, rich mahogany, and *L. mitissimus*, golden tawny, all arrest the eye as it wanders over mossy undergrowth.

The genera *Bolbitius* and *Coprinus* are not without aesthetic interest. Both have to be enjoyed when young, as they share the habit of quickly liquefying and shrivelling up; both flourish on dung and rich soil. The species of *Bolbitius* are delicately conical and striped, usually tinted yellow. The Coprini are white, silvery grey, dark brown or black. *Coprinus comatus* appears in shaggy egg-like flocks; *C. micaceus*, densely tufted and date-brown, glistening with shining particles, lives apart from its dung-loving brethren on decaying stumps and roots.

In accordance with the classification of the Agaricales adopted by Mr Carleton Rea, I now dwell for a moment on *Marasmius*. We all know the famous fairy rings formed by *M. oreades*, and appreciate the intriguing charm of the circular arrangement in which these little pale brown caps appear. *M. peronatus*, gloomily emerging from fallen leaves in darkling woods, attracts with the dense covering of white or yellow hairs on the lower end of the stem; *M. hariolorum* makes an appeal with its reddish to white companies of densely crowded caps on relatively long stems. The minute *M. ramealis* in regiments on fallen twigs never fails to please, while *M. alliaceus* with its milk-white cap and stiff black stem is curiously attractive to me on account of its strong smell of garlic. I am not fond of the smell of garlic, and possibly my reason for appreciating it in this fungus is that it is a feature which makes identification easy, and, in a genus full of species which shade off one into the other, any unmistakable evidence, however disagreeable in itself, becomes pleasureable.

I would like to dwell on *Panus torulosus*, *P. stypticus* and *Lentinus cochleatus*, but the Cantharellineae are beckoning and I hasten to speak of *Cantharellus cibarius*. If I had to appraise the toadstools as flowers are judged at a horticultural show, I would give *C. cibarius* maximum points for colour, form and smell. Its rich clear yellow is delightful, as is the graceful undulation of its lobed pileus. The thick, distant gills stream down the stem, running one into the other. The

smell is deliciously suggestive of apricots. It differs greatly from its common relative *C. tubaeformis* which pleases with its trumpet-like shape and strange mixtures of dark orange, yellow and black. *Craterellus cornucopioides* violently ejected from its former association with the Thelephoraceae, follows hard on its heels. Never was fungus more descriptively named; a cup and a horn of plenty. True, it is blackish grey with a prevailing tone of ashes, but it is attractive even as is silver streaked with black. It sometimes occurs in great quantities and then disappears for many seasons; it is said to be good to eat.

With a passing glance at the rare *Neurophyllum clavatum* of lilac hue, which I once found in Epping Forest, although its habitat is said to be mountainous fir woods, I will go on to the Boletineae.

In deference to the views on classification supported by Mr Rea, I say a word here about the genus *Paxillus*. It is not within the scope of this address to discuss the reasons for placing a fungus which has gills among those whose hymenium lines the insides of tubes, which is a distinguishing feature of the Boletineae. Among the Paxilli, *P. involutus* is the only common species. It pleases with its dark yellow regular cap and the beautiful manner in which, in its early stage of development, the margin of the cap is tightly rolled inwards. As in the related species, the gills are easily removed from the horny base of the pileus, and this feature is a useful aid to identification.

This is the appropriate point at which to mention *Strobilomyces strobilaceus*, the very pleasing fir-cone boletus. I have seen it only once, at our Worcester meeting fifteen years ago, and then it was past its prime. It is like *Boletus*, but it has a cap shaggy with dark scales, and the stem is also scaly below a ring. It is a pity that this intriguing fungus is not more plentiful.

As a rule the Boleti do not attract me very much—the caps are frequently of dull colour and then look like lumps of dirty dough. The stems are often irregularly and unevenly swollen. There are some exceptions and I hasten to make my apologies to *B. elegans*, the richly golden fungus that frequents coniferous woods and lights up the needle-strewn ground. It is remarkable how it follows conifers. Epping Forest is a large area of mixed woodland where conifers are represented only by a clump of about twenty larch trees on the northern edge, but *B. elegans* comes up there. The very common *B. chrysenteron* is a favourite of mine because of the way the pellicle of the pileus cracks into patches with red interstices; the stem too is often brilliantly coloured. *B. versipellis* is a tall, handsome object with its large yellow cap and grey tapering stem, and *B. scaber*, in spite of its speckled grey and black can be graceful. The great attraction of this genus is the rich blue or indigo colour to be seen when the inside flesh is suddenly exposed to the air. Examples are afforded especially by *B. badius*, *B. luridus* and *B. erythropus*.

The Polyporaceae are not conspicuous for aesthetic attraction. To me some of them are just repulsive, and only a sense of fairness to the unfortunate, or shall I say scientific impartiality, will induce me to look at them. *Fomes fomentarius* with its great ugly hooves and sickening odour is a case in point. I turn with relief to some of the exceptions in the genus *Polyporus*.

There is dainty little *Polyporus perennis* with its central stem; *P. nummularius*, *P. picipes* and *P. varius* are also an attractive group among the species with thin caps and well-marked stems. There is a rough, jolly beauty about *P. squamosus*. I like the bold way in which it thrusts out its great scaly yellow caps from the trunks of trees, and its odour, suggestive of cheese and beer, is refreshing. I am always pleased to come across *P. intybaceus*—the hen of the woods. It is a compact mass of overlapping rosettes bearing some resemblance to a grey grouse hen. To quote Mrs T. J. Hussey: "The heap of overlapping pilei is relieved with zones of a deeper shade, and the under surface is snowy-white like the bird's down when she angrily elevates her feathers." The fungus is rather rare in Britain, but is said to be common in the Rhenish forests, the Vosges and the Ardennes. Perhaps the most colourful species of *Polyporus* is *P. sulphureus* which projects from the trunks of many kinds of trees its reddish yellow or orange caps, sometimes in pleasing undulating masses. The great date-brown and zoned overlapping plates of *P. giganteus*, when allowed to grow undisturbed, also make a picture. *Ganoderma lucidum*, the sealing wax fungus, is remarkable for its polished mahogany pileus extending sideways into its similarly coloured stem. We all know and appreciate the beauty of *Polystictus versicolor*. It is variously coloured as its name implies. At its best it forms a circular tuft of thin, overlapping pilei, densely velvety, shining, and zoned with shades of grey, green, brown or orange.

There are many more fungi which make an aesthetic appeal, but this address has already reached to sufficient length so I must content myself with a brief reference to the many which ought to be mentioned. I once met *Hydnum erinaceus* hanging in the hollow trunk of an old hornbeam and resembling masses of long white stalactites. There is a charm about many of the Hydnums. Although *H. repandum* seems unpromising when seen flat on the ground in irregular yellow masses, it has only to be turned over to reveal the fascinating mass of small, creamy white spines; and what can be daintier than the little *H. auriscalpium* with its reniform pileus and dark spines borne on a fallen pine cone?

Stereum hirsutum covering an old log can provide a bright stretch of ochre. The genus *Clavaria*, so well known for its erect receptacles, singly or in tufts, has many noteworthy species. Those of our members who visited Moccas Park, in Hereford, ten years ago will still remember

the lovely masses of the violet *Clavaria amethystina* and the ivory white *C. Kunzei* which we found there, and we all delight to meet the many yellow forms which leave us doubting how to name them.

I will conclude with a few words on some of the Ascomycetes. The most outstanding for beauty is the reddish orange *Otidea aurantia*. Its brilliant cups spread out on sandy soil always delight the eye. Then there is the strange *Helvella crispa* with its wavy irregular cap and drooping lobes and the still stranger *H. lacunosa*, blackish grey, arising from black leaf mould.

Last, and quaintest of all, the Morels, *Morchella esculenta*, *M. crassipes* and others, which are always in the minds of those who attend Spring Forays and frequently nowhere else. Our visit to Gloucestershire in 1934 was rewarded with the discovery of troops of *M. crassipes* and the fortunate members who were there enjoyed the sight of those strange, oblong tawny caps pitted with deep holes and borne aloft on stout inflated stems.

There must be some four thousand species of Basidiomycetes alone. There are those among us who would like to boil them down to one thousand, others who think they should be increased. Comparatively few are common and the prospect of finding a fungus seldom met with or never seen before, a fungus delicate of perfume, rich in colour and beautiful in form, is sufficient to maintain our interest and tempt us out on journeys to all corners of these islands.

AGARICS. NEW RECORDS AND OBSERVATIONS

By A. A. PEARSON, F.L.S.

(With Plates I–III)

The following are a few of the more interesting species of agarics that I have observed during recent years. There are many others which I hesitate to record and which require further study. Three of the records have already been published in the *Essex Naturalist*, and one in the *Naturalist*. It is satisfactory to be able to add several species of *Russula* to the British list. The study of this genus has been rendered much easier by the publication of several monographs by European mycologists, and I am especially indebted to the most recent one, *Russula-Monographie* by Julius Schaeffer, who has dealt with the genus in a very helpful manner. His work may be referred to for a more complete synonymy than I have thought it necessary to include.

The spores of *Russula* have been examined in chloral iodine under a high-power oil immersion lens, without which the ornamentation is not clearly seen. The cystidia have been examined in sulphovanillin. At first I had difficulty because sulphovanillin emulsifies, but Prof. René Maire kindly explained his method of dealing with this difficulty. A few vanilla crystals are placed in a watch-glass, a little sulphuric acid added and these are mixed with a glass rod. The mixture can be poured into a bottle with a glass stopper but after a time it is liable to emulsify and must be freshly made when next wanted.

Pluteus gracilis (Bres.) Lange, "Studies in the Agarics of Denmark. III," in *Dansk Bot. Ark.* II, Nr. 7. (1917), 6.

P. pellitus Pers var. *gracilis* Bres. in *Hedwigia*, XXIV (1885), 134.

Pileus 1–4 cm. diam., semi-globose then flat, about 1 cm. thick, fleshy, soft, dry, white with brownish centre when old, silky fibrillose, cuticle separable, margin straight. *Gills* crowded, free with clear space in fully expanded specimens, broad, 6 mm. in average size, rounded near margin, thick, pink with edge sometimes darker. *Stem* short, 3–4 cm., solid, white, smooth, minutely fibrillose. *Basidia* 4-spored. *Spores* in mass pink, broadly oval, $6\frac{1}{2}$–$7 \times 5\frac{1}{2}$–$6\,\mu$ smooth. *Cystidia* on edge and face of gills, broadly fusoid, 12–16 μ wide with blunt apex. Hyphae of cuticle septate, 10–20 μ diam. *Taste* mild. No smell.

This species looks exactly like a small mushroom (*Psaliota campestris*) and peels in the same way. It cannot be placed as a variety of *Pluteus pellitus* which has hooked cystidia.

Astrosporina decipientoides (Peck) n. comb.

Inocybe decipientoides Peck (1907) sec. Kühner & Boursier in *Bull. Soc. Mycol. Fr.* XLVIII (1932), 141.

Inocybe globocystis (Velen.) Heim, *Le Genre Inocybe* (1931), p. 326 and pl. 26, fig. 3.

Pileus 1–3 cm. thin except in centre, conical then expanding round the persistent umbo, brown-ochraceous, bay-brown in centre covered with dense adpressed radial silky fibrils which deepen in colour and separate into shaggy squamules, when old showing the white flesh underneath; umbo smooth or showing traces of the tomentose veil. *Gills* crowded or subdistant, fairly wide, thin, cream then ochraceous, ventricose, sinuate, adnexed or sometimes adnate the whole width of gill. *Stem* 2–4 cm. long, 3–5 mm. thick, white at first, then pale ochraceous or reddish brown under the fibrillose surface, white pruinose at summit, solid. *Spores* angular oblong, 8–10 × 5–8 μ with pentagonal profile. *Cystidia* on edge and face of gill pyriform or globular, usually muriculate at apex, which is papillate or narrow-elongate or blunt, hyaline, very variable in size, average about 45 × 20 μ (–40 μ). *Flesh* grey when wet, white when dry. *Smell* unpleasant or none. *Taste* mild.

Habitat: on the ground solitary or in groups, among grass on paths in woods.

Henley, Sussex, 21 September 1932; Saxonbury Woods, Sussex, 2 August 1934; Epping Forest October 1934.

This species is not uncommon, and is chiefly characterized by the bulbous cystidia. These are however mixed with cystidia of more normal shape.

Astrosporina napipes (Lange) comb. nov.

Inocybe napipes Lange, "Studies in the Agarics of Denmark. III," in *Dansk Bot. Ark.* II, 2, Nr. 7 (1917), 4414.

Pileus 2½–5 cm., conical or expanded, with a conical umbo, brown or dark ferruginous, somewhat paler at the margin, fibrillose-rimose, the yellowish flesh showing beneath. *Gills* somewhat crowded, pale grey at first, turning brown with the spores, more or less ventricose, adnexed, edge minutely floccose. *Stem* 5–7 cm. long, fibrillose, pale above, brown or ferruginous below, with clearly-defined white bulbous base. *Spores* brown, 8–9 × 6–7 μ, angular, with conical protuberances. *Cystidia* fusoid, ventricose, muriculate at the apex, 50–60 × 13–18 μ.

Habitat: on moist ground in deciduous or coniferous woods.

In open space of pine woods, Hubberholme, Wharfedale, Yorkshire, 7 September 1936.

This species is probably not uncommon, but has been confused with *Astrosporina asterospora*, which has a pileus more definitely rimose,

and star-shaped spores instead of the slightly elongate spores of the present species. The separation off from *Inocybe* of the species with warted spores to form the genus *Astrosporina* is not generally followed. I have adopted the genus according to the practice of Carleton Rea's "British Basidiomycetae" principally for the sake of uniformity.

Tricholoma Inocybeoides n.sp., Plate III.

Pileus 1–3 cm., grey with whitish bloom, acutely umbonate, umbo dark with purplish tinge, edge incurved at first, silky, fibrillose with greyish brown adpressed fibrils, fleshy in centre, membranous near periphery. *Gills* crowded, white turning yellow, deeply emarginate, ventricose 2–3 mm. wide. *Stem* 2–3 cm. long, 4–5 mm. thick, solid then hollow, at first white with slight reddish tinge below, finally stained yellow. *Basidia* narrowly club-shaped, about $20–25 \times 4\frac{1}{2}–5\,\mu$. *Spores* hyaline, ovate $4\frac{1}{2} \times 2\frac{1}{2}\,\mu$ ($4\frac{1}{2}–6 \times 2\frac{1}{2}–3\,\mu$). *Smell* strong, unpleasant. *Taste* mild.

Charlton Forest, Cocking, Sussex, 22 September 1932.

Latin diagnosis:

Tricholoma Inocybeoides Pearson

Pileus 1–3 cm. latus e convexo explanatus, acute umbonatus, umbone obscuro tincto purpureo, griseus albo-pruinatus, fibrillosus, margine primitus involuto; caro carnosa in medio, membranacea ad marginem. Lamellae confertae, albae demum flavo-maculatae postice emarginato-uncinatae 2–3 mm., latae. Stipes teres 2–3 cm., longus, 4–5 mm., crassus, griseus e farcto cavus. Sporae hyalinae, ovatae $4\frac{1}{2} \times 2\frac{1}{2}\,\mu$ ($4\frac{1}{2}–6 \times 2\frac{1}{2}–3\,\mu$.). Basidia clavata $20–25 \times 4\frac{1}{2}–5\,\mu$. Odore nauseoso. Sapore vix sensibili.

Hab: in nemoribus frondosis vel mixtis autumno.

This plant looks strikingly like a small whitish *Inocybe* with a dark umbo. It belongs to the "terreum" group of *Tricholoma*, the yellowing of the gills suggesting *T. argyraceum* from which it differs chiefly by the smaller size, the acute umbo, small spores, and strong unpleasant smell.

The sketch of *T. Inocybeoides* on Plate III, has very kindly been made by Miss E. M. Wakefield, M.A., F.L.S.

Entoloma excentricum Bresadola, *Fungi Trident*, I, p. 11, tab. VIII (1881) and *Icon. Myc.* Tab. 556; Konrad & Maublanc, *Icon. Sel. Fung.* pl. 191.

Pileus 1–6 cm. convex then expanded, usually umbonate, but sometimes flat and finally depressed in centre, pale dull ochraceous (very dilute *café au lait*), whitish near margin, glabrous, edge incurved at first. *Gills* subdistant, emarginate, wide, ventricose, white then pink; edge serrate. *Stem* 4–7 cm., usually excentric but often central, white then pale ochraceous, primrose above, solid then hollow, slightly

thickened at base. *Spores* pink, nodulose, 10–14 × 7–8 μ. *Cystidia* on edge hyaline, lanceolate, ventricose, 40–70 × 10–18 μ. *Smell* faint of meal. *Taste* mild.

Habitat: in grass lands at the edge of woods. Autumn. Cocking Down, Sussex, 22 September 1932.

Our specimens correspond to the figures of the Konrad and Maublanc plate where the acute umbo shown in Bresadola's figures is absent. A doubt may be expressed whether these represent the same species.

Hebeloma subsaponaceum Karst., *Symb. Myc. Fenn.* XIII (1884), 3.

Pileus 4–5 cm., expanded, flat, light ochre (biscuit-colour), minutely fibrillose under lens, looking quite bald and shining when dry, edge crenate. *Gills* darker than pileus, distant, edge irregularly wavy, narrowed near stem, wide and rounded near edge of pileus, 10 mm. wide in middle. *Stem* 8–10 cm. long, 7–8 mm. thick, same colour as pileus, longitudinally fibrillose and striate with adpressed fibrils, cylindrical, solid, flesh white above, rufous below. *Spores* almond-shaped, granulate or 1-guttulate, smooth, about 14 × 8 μ. *Smell* strong of soap. *Taste* mild.

Hulme Park, Northumberland, 19 September 1933, during the Newcastle Foray.

Hygrophorus (Limacium) lucorum Kalch., *Icon. Select. Hymen.* (1874). p. 35, t. 19, f. 3.

Pileus 2–6 cm., lemon-yellow with reddish tinge in centre, primrose and almost luminous with minutely flocculose remains of veil, viscid then dry, convex, at first umbonate, the umbo sometimes flattening out, flesh thin, margin involute then straight. *Gills* subdistant, creamy white but usually turning yellow near the margin of pileus or sometimes completely, rather thick, adnate-decurrent. *Stem* pale lemon-yellow, longitudinally fibrillose with white veil, subviscid, solid, slightly thickened or pointed at base. *Spores* ellipsoid apiculate, 7–9 × 4½–5 μ, 1-guttulate. Flesh white, lemon-yellow under cuticle. No smell or taste.

Habitat: under or near larches.

In grass near clump of larches, Frant Bottom, near Frant, Sussex, 4 November 1933; in grass near larch wood, Buckhurst Park, Sussex, 23 October 1934.

Collybia pseudo-clusilis Josserand & Konrad in *Bull. Soc. Lin. Lyon.* (1931) 21; Konrad & Maublanc, Icon. selectae fungorum, Pl. 207, ii.

Pileus 1–3 cm., semi-orbicular with centre sometimes slightly depressed, sub-membranaceous, hygrophanous, soft grey with brownish

striations, when fresh striate to the disc, darker in the centre, white silky opaque when dry. Pellicle somewhat viscid and separable when dry. *Gills* sub-distant, broad, up to 5 mm., thick with blunt edge, often veined at base, white or pale pinkish, ventricose or straight, emarginate with decurrent tooth, edge straight or undulate. *Stem* 1½–2 cm. long, 1–1½ mm. thick, greyish white, darker at base, soft but not fragile, glabrous or slightly fibrillose.. *Spores* white in mass, broadly ovate, mostly $7 \times 5\,\mu$ ($6\frac{1}{2}$–$8 \times 4\frac{1}{2}$–$5\,\mu$), 1-guttulate. *Cystidia* on gill edge thin-walled, cylindrical, obtuse, varying in size, 40–70 × 9–12 μ. No smell or taste.

Habitat: on ground under coniferous trees, in late autumn or winter.

Broadwater Forest, Sussex, end of November 1933; Drayton Brecks, near Norwich, Norfolk, November & December 1935. (G. J. Cooke.)

When I first gathered this, I wished to name it *C. cessans* (Karst.) Fr. which is placed next to *C. clusilis* by Fries in "Hymenocytes Europei". The name *cessans* (=linger or delay) would be peculiarly suitable for a species that appears so late in the season. However, Fries in his description refers the species to "*A. stoloniferi* var. *Fr. Epicr. p.* 92". This is a puzzling reference, since there is no mention of *A. cessans* in the Epicrisis and *A. stolonifer* is placed by Fries in the section Laevipedes, while he puts *A. cessans* in the Tephrophanae. However, as there is certainly no relation between our species and *Collybia stolonifera* which presumably is the same as *C. esculenta* (Wulf.) Fr. it is better to adopt a name that gives rise to no dispute. Fortunately the species has been clearly described by Josserand and Konrad under the name *C. pseudo-clusilis* which Mr Rea has advised me to adopt.

Mr J. E. Lange has also informed me that the species published by him under the name of *C. cessans* Karst. is not the same as *C. pseudo-clusilis* Josserand & Konrad. The identification of these small grey hygrophanous agarics is beset with difficulties. Many of them are transitional forms which might be placed either in *Clitocybe*, *Omphalia* or *Collybia*. It is satisfactory to have another of them defined with sufficient clearness to enable us to give it a name.

Collybia clusilis Fr. differs in having larger spores, no cystidia on the gill edge, and is without the viscid pellicle.

Collybia cessans Karst. sensu Lange differs in having subglobose spores; the marginal hairs on the gill edge are more slender and it lacks the viscid separable pellicle. This species has much in common with *Omphalia striaepilea.*

Leptonia sarcita (Fr.) Quél., Champ. Jura Vosges, *Bull. Soc. Sci. nat. Rouen.* (1879), p. 156.

Pileus usually about 2 cm. (up to 4 cm.), hygrophanous, thin, semi-globate, with small umbel in centre, waxy brown, distinctly

striate when moist, paler, livid and barely striate when dry when the surface has a silky polish. *Gills* sub-distant, adnate, sinuate or sometimes almost decurrent, broad and fairly thick, greyish at first then pink. *Stem* solid then hollow, slender, polished, smoky white, woolly at base. *Flesh* of pileus pale greyish buff. *Spores* pink, polygonal 8–11 × 7–8 μ. Basidia 4-spored, 25–35 × 8–9 μ. No marginal hairs or cystidia. No smell or taste.

Habitat among the grass on the edge of deciduous woods. Stratton Strawless Woods, Norfolk, 4 October 1934; Sheffield Park, Sussex, 7 October 1934; Wadhurst, Sussex, June 1935.

Not uncommon. I have gathered this species on many previous occasions, but never identified it satisfactorily till Konrad & Maublanc published figures and an excellent description in their *Icones Selectae Fungorum*, pl. 183.

Naucoria (Alnicola) submelinoides Kühner var. ***alnetorum***, R. Maire in *Bull. Soc. Mycol. Fr.* XLVII (1931), 242, and XLVI (1930), 223.

Pileus 1–3 cm., convex, edge inturned at first, then flat, finally turned up, hygrophanous, thin, fragile, watery bay-brown, darker in centre, drying to biscuit-colour, striate when moist, scurfy when dry, margin straight; flesh honey-colour. *Gills* subdistant or distant, adnate, rather wide, ventricose or triangular, thin, pale honey-colour, edge flocculose, numerous smaller gills. *Stem* 3–5 cm., long, 2–4 mm., thick, fairly firm with internal pith, honey-coloured above, bay brown or almost black near base, fibrillose striate. *Basidia* 2-spored, sterigmata about 8 μ long. *Spores* in mass ochraceous, almond-shaped 13–16 × 6–7 μ, minutely verrucose. *Hairs* on sterile edge of gill, claviform, thin-walled, 50–70 × 7–9 μ. *Taste* mild. *Smell* musty (of meal sec. Maire)

Differs from *Naucoria escharoides* in the darker colour, distant gills and club-shaped cells on gill edge.

Habitat: in swamps under alder. Found in quantities near Benhall Mill, Tunbridge Wells, October 1936.

This species is probably fairly common, and I have observed it in other localities, always with 2-spored basidia. According to Maire it may have occasional basidia with 3 or 4 spores. The species was originally described as with 4-spored basidia by Kühner in *Le Botaniste*, XVII (1936), 175 when he introduced the new genus *Alnicola*, to include species of *Naucoria* with large verrucose almond-shaped spores similar to those found in *Naucoria escharoides*.

Mycena uracea, n.sp., Pl. III.

Pileus 1–3 cm. at first conical then expanded, umbonate, finally with edge upturned, umbo usually persistent but sometimes absent, smoky grey, darker in centre, sometimes brown or black, sulcate,

fleshy in centre, membranous towards edge. *Gills* distant, ventricose, uncinate, dirty white or grey, when old with a pink tinge, edge straight or minutely flocculose. *Stem* normally 2–3 cm. long, sometimes with a long rooting base, polished, often with white villose down at base, cartilaginous, hollow, reddish grey at apex. *Basidia* 2- or 4-spored 40–50 × 7–8 μ. *Spores* hyaline, broadly ovate, apiculate, 8–9 × 6–6½ μ, (11 × 8 μ), 1-guttulate or granular. *Cystidia* abundant, globose, warted, mostly about 20 μ across, with occasional smaller or larger sack-shaped cystidia also warted, lining the gill edge. *Smell* none. *Taste* somewhat rancid.

Broadwater Forest, Sussex, October and November 1933; Weybridge, Surrey, 1920. Hindhead, Surrey, October 1937.

On burnt ground, usually attached beneath the soil to the burnt roots of heather. Not to be confused with dark varieties of *Mycena galopus* often growing in the same habitat.

Latin diagnosis:

Mycena uracea Pearson

Pileus 1–3 cm., latus, conico-expansus, umbonatus, umbo plerumque persistens, interdum absens, margine demum revoluto, griseo-cinereus centro obscuriore, vel fuscus interdum niger, sulcatus, carnosulus in medio, membranaceus ad marginem. Lamellae distantes, uncinatae, sordido-albae vel griseae, demum leviter roseo-tinctae, ad aciem leves vel subtiliter fimbriatae. Stipes solito 2–3 cm. longus saepe in basi radicatus, glaber, basi albido-villosa, cartilaginosus, cavus, rufo-griseus apice pallido. Basidia cum 4-vel-2 sterigmatibus. Sporae late-ovatae apiculate 1-guttulate vel granulatae 8·9 × 6–6½ μ (11 × 8 μ). Cystidia globosa, verrucosa, maxime circa 20 μ diam. Odore nullo. Sapore subrancido.

Habitat: in terra ambusta ad radices ericetorum.

The sketch of *Mycena uracea* on Pl. III, for which I am indebted to Mrs Violet Astley Cooper, depicts typical specimens of average size.

Galera plicatella **Peck** in *Ann. Rep. N.Y. St. Mus.* XXIX (1878), 66.
Agaricus coprinoides Peck in *Bull. Buffalo Soc. Nat. Sci.* 1 (1873), 52.
? *Bolbitius luteolus* sensu Ricken (1915, *Blätterpilze*, p. 52).
Conocybe plicatella (Peck) Kühner (*Le Genre Galera*, p. 137).

Pileus 5–15 mm., membranous, hygrophanous, at first semiglobate or conical, then flat, usually papillate, light ochraceous, dark in centre, polished and slightly viscid at first, minutely plicate, splitting when old. *Gills* light ochraceous with pale edge, subdistant when young, distant when old, straight or somewhat ventricose. *Stem* 1–1½ mm. thick, white, flocculose, striate *sub lente*, hollow, thickened at base into a small bulb. *Spores* ovate, mostly 8 × 5 μ (7–10 × 4½–6½ μ), with germinating pore, often guttulate. *Basidia* 4-spored, club-shaped

with narrow base, about $20 \times 8\,\mu$. *Cystidia* on gill edge abundant, 30–60 μ long, thin-walled, filiform with swollen base, 8–10 μ wide, and apex obtuse; similar cells on stem; surface of pileus made up of globose or balloon-shaped cells 10–16 μ wide. *Flesh* of pileus ochraceous, of stem white or pale honey-colour. No smell or taste.

Habitat: on lawn, Kent every year since 1925, in August and September; on lawn, Hampshire, September 1935.

This is probably a common species in England, as it is in France, though it has only recently been recorded by R. Kühner in his excellent monograph of the genus *Galera*. It appears on lawns after the first summer rains and continues for weeks. It is easily recognized by the pubescent white stem with the bulbous base and the pale ochraceous pileus with the darker centre.

Pleurotus ulmarius (Bull.) Fr.

On 10 November 1934 a specimen was sent to me by Mr C. H. Grinling who gathered it on Woolwich Common. It was growing high up on an elm tree. Unfortunately it was not cut near the base of the stem, so the complete fruit body was not secured. Its gigantic size was, however, so striking, that I thought it worth while having a photograph made (see Pls. I and II). The pileus is not fully unfolded, but even in this stage the width was 25 cm., and the oval stem 8×5 cm. With more freedom to expand, the width would have been at least another 10 cm. which would have made it 35 cm. (14 in.), so in descriptions of this species the limits of size should be from 6 to 35 cm. The weight was 2 lb. 6 oz. (1·08 kg.).

The pileus was a dirty white with a yellowish tinge. The cuticle was cracked in the manner characteristic of the species, and the tesselated marble-like surface comes out well in the photograph. The gills were a pale smoky or soapy white, with wavy edge and the whole gill corrugated by pressure. It will be noticed how variable the gills are in width and in their attachment to the stem. On one side the gills are 22 mm. at the widest place, and are broadly adnate to the stem; on the other side the gills are very narrow, only 10 mm. in the widest part, and 3 mm. near the stem, adnexed, subdecurrent or free.

The stem was practically central. The colour was a dirty yellowish white with longitudinal rugulose raised lines.

The flesh was pure white and firm, very like that of *Boletus edulis*, and it should be mentioned that the gills could be taken from the pileus like the tubes from a *Boletus*.

Taste mild; smell of new meal. *Spore* deposit pure white. *Spores* globose, 5 μ, or subglobose, $5\frac{1}{2} \times 4\frac{1}{4}\,\mu$ often 1-guttulate, smooth, non-amyloid (not turning blue with iodine). *Basidia* 4 spored, $30–40 \times 6–6\frac{1}{2}\,\mu$. *Cystidia* none.

Pleurotus ulmarius was originally described by Bulliard who also

described a species which he named *P. tessulatus*. This is probably the same species with the cracked marmoreal surface well defined as in our specimens.

Russula vesca Fr.

In the old days, if the stem of a *Russula* had a tendency to stain brown, it was regarded as *R. vesca*. Forms of *R. atropurpurea* were often mistakenly referred to this species. *R. vesca* is a species easy to recognize when true to type, but sometimes it occurs in very puzzling forms. It is closely related to *R. heterophylla*, having similar small spores with shallow protuberances. It is one of the first Russulas to appear in England after the summer rains, when it is abundant in some districts, usually in oak-birch woods. It continues sporadically through the autumn.

Cooke's plate 1002 (1075) is very unsatisfactory and depicts either a very untypical form of *R. vesca*, or another species.

Rea's description is good, but a few additional details will be found helpful:

Pileus 5–12 cm. diam., at first semiglobate, then flatter with depressed centre, pale pink flesh-colour (K6, D7 and 8 Lange's chart) often dark in centre, paler or white round margin, sometimes with a dirty brown tinge or with rusty spots, rather slimy and polished when moist, mat when dry, smooth in centre, radially wrinkled towards edge, especially noticeable *sub lente*; the cuticle which can be peeled half way to the centre often not quite reaching the edge, and a very thin marginal line of white flesh is seen; sometimes the cuticle is cracked towards the sulcate margin. *Gills* white, sometimes (but not always) weeping, which causes the edge to be thickly studded with rusty spots, narrowed near the stem but broader towards the edge, and often growing beyond the cuticle of the pileus, thin, not brittle, forked, very crowded and more or less decurrent. *Stem* white, rarely with a pink tinge, often spotted with rusty spots, especially near the base, firm, either very short of normal length, rugulose, cylindrical or with attenuated base, sometimes spreading out towards the top, causing the gills to be decurrent. *Spores* round, ovate or almost pear-shaped, with shallow isolated warts which may cover the surface or be sparse, very thin lines occasionally visible, $5–8 \times 5–6\,\mu$. *Cystidia* fusiform or blunt, sparse on face of gills, abundant or sparse on edge, turning blue with sulphovanillin; similar cystidia sometimes sparsely scattered on cuticle of pileus. *Flesh* white, often with rusty spots. *Taste* mild, nutty. *Smell* said to be sometimes fishy when old.

Chemical reactions: with ferrous sulphate, pink; with phenol, none at first, then brownish red.

Spore mass white or, if heaped up, very pale cream-colour (B of Crawshay's chart).

Russula aurora Krombh. *Natur. Get. Ab. u. Beschr. Schwämm*, IX, 1845, p. 11, Tab. 66, figs 4–7.

Pileus 3–10 cm. wide, convex then flat and depressed in centre, fairly thick, firm, viscid then dry, cuticle separable, surface mat and granular under a lens, very variable in colour, a rich creamy yellow, mixed with rusty tints, in fact all the colours of a ripe peach (Lange's chart: e5, 7, 8, j4), margin regular, at first incurved, rarely tubercular; flesh white. *Gills* crowded, thin, edge smooth, straight, broad and rounded near margin of pileus, narrowed towards stem, often forked from base, white, then pallid cream. *Stem* 4–8 cm. long, 1½–2 cm. thick, straight or curved, base thickened usually, firm surface veined, white; flesh white. *Spores* in mass pale cream (B to C of Crawshay's chart), ovate, 8–9 × 7–8 μ, with prominent apiculus and shallow warts joined up with thick or faint lines showing partial reticulation. *Cystidia* on gill edge sparse, blunt (club-shaped), not turning blue with sulphovanillin; no cystidia on pileus. *Taste* mild, then rather bitter. *Smell* none.

Chemical reaction: with sulphovanillin a brilliant carmine red, with ferrous sulphate, faint salmon pink.

Habitat: deciduous woods, mostly under beech, Mayfield, Sussex, 9 October 1935; in mixed wood under beeches; Buckhurst Park, Sussex, 2 August 1936.

The colour reaction when sulphovanillin is applied to the flesh is a sure indication of the species. Schaeffer identifies the species with *Russula rosea* Quél. as described by Crawshay who points out the sulphovanillic reaction. The colour of the pileus, according to Crawshay, varies from pink and yellow to a purplish brown, which corresponds to the specimens gathered at Buckhurst Park.

Russula aurora has been recorded by Rea as a variety of *R. lepida*, but though with a mat surface to the pileus, it is not powdery and is distinct in many details.

Russula versicolor J. Schaeffer in *Z. f. Pilzkunde* (1931); *Ann. Mycol.* XXXI (1933), 369 and XXXII (1934), Tab. II.

Pileus 1½–6 cm., at first convex, then with centre depressed edge upturned, thin but consistence fairly firm, cuticle at first viscid, peeling half way to centre, smooth, polished, colour very variable; with suffused mixture of brown, violet, yellow and usually with green in centre; sometimes the green is very prominent, with pale margin and violaceous centre; margin straight and regular, when old closely tuberculate; flesh white. *Gills* crowded at first, subdistant later, cream, rounded at margin of pileus, narrowed to point towards stem, almost free, fairly wide (7 mm. in larger specimens) edge thin, mostly one size, a few shorter. *Stem* 2–5 cm. long, 8–15 mm. thick, equal or thicker above, consistence firm, spongy inside, dry, veined white,

slowly turning yellow, but not always; flesh white, turning yellow. *Spores* in mass ochre (near E and F of Crawshay's chart), ovate with prominent warts and net-like reticulations, apiculus prominent, 8–9 × 5½–6 μ. *Basidia* 4-spored, 25–40 × 8–10 μ. *Cystidia* abundant on gill edge, sparse on face, 50–80 × 8 μ, turning blue with sulphovanillin. *Taste* acrid, especially the gills. *Smell* faint, fruity odour.

Chemical characters: flesh pink colour with ferrous sulphate.

Habitat: under birches, Broadwater Forest, Sussex, 14 September 1935, 1 August 1936; Epping Forest, Essex, 10 September 1936.

Herr J. Schaeffer confirmed the 1935 specimens as "Versicolor wie sie leibt und lebt, absolut sicher noch am Exsiccat zu erkennen, besonders durch die länglichen cretierten Sporen!"

This species is probably common in England. Hitherto it has been confused with *R. puellaris* which is mild in taste, soon completely suffused with yellow and has spores with isolated warts or occasional fine reticulations. Also the greenish tinge which is so frequent in *R. versicolor* rarely occurs in *R. puellaris*.

Russula xerampelina (Schaeff.) Fr.

Apart from certain species closely allied to *Lactarius* such as *Russula nigricans*, *R. densifolia* and *R. albo-nigra*, this is the only species of *Russula* where the flesh turns a dark green when ferrous sulphate is applied. This reaction, which was discovered by Melzer, has made the determination of *R. xerampelina* easy. The species is extremely variable, and a study of its many forms may be left to a later date. They all agree in certain details that can be observed in the field, such as the fishy smell, especially when old, and the brown discoloration of the stem when handled. The spores are round or broadly ovate, 8½–13 × 8–11 μ (average measurement given by Crawshay 9 × 10 μ) with prominent warts and extremely thin anastomosing lines barely visible under the high power of the microscope.

Among the forms or varieties may be mentioned the following which have already been recorded in Britain:

R. erythropus (Fr.) Peltereau.

R. Barlae Quél.

R. olivascens Fr. (*R. alutacea* var. *olivascens* (Fr.) Rea).

There are also colour forms resembling *R. fusca* and *R. mustelina* which on closer examination are found to be *R. xerampelina*.

R. Duportii Phill. may also be this species.

The smell is variously described as quite pleasant when fresh, and when old as being like crab, lobster, cooked shrimps or herring.

Russula claro flava W. B. Grove in *Midland Naturalist* (1888), p. 265.

It is desirable to clear up the identity of this much disputed species. It is strange that the species of a mycologist still living should be in

doubt. Cooke in his *Illustrations of British Fungi*, pl. 1198 (1196) called it *Russula ochroleuca* var. *claroflava* Grove, and as the drawings in the upper part of the plate are signed W.B.G. we may take them as representative of the species. Rea has accepted the view that the species in question is only a variety of *R. ochroleuca*.

Several European mycologists have written to me about the matter, and the obvious thing to do was to communicate with W. B. Grove himself. He died early this year, shortly after the publication of the second volume of his *British Stem and Leaf Fungi*. In the early days of his botanical career he was interested in the agarics, but had not been prominent in the study of this group for many years. In March 1933 I received the following letter and description in reply to my request for a clearer definition of *Russula claroflava*:

16 March 1933

Dear Mr Pearson,

Dr Bayliss Elliott has handed me your letter of 7 March, and asked me to answer your queries. Herewith I send you a copy of my original description from the *Midland Naturalist*. (Alas! it has ceased publication for many years.)

I am pleased to hear that you find *Russula claroflava*; I think it is unmistakable, but I fancy I have suffered through three successive errors on the part of three editors:

(1) Cooke reproduced the coloured sketches which I sent to him, in his *Illustrations*, but unfortunately he added a figure of his own which is not at all the same species; also he did not get the colouring of his plate as bright as my sketches.

(2) Massee in his *Fungus Flora, added* the word "acrid", which is incorrect; *R. claroflava* is perfectly mild.

(3) When I sent the additional note on the species to the *Journal of Botany*, in 1920, the Editor (Mr Britten) altered the word "*mild*", which I put at the head of the description, into *mihi*.

I will now answer your questions:

(1) No, it is *not* a variety of *ochroleuca*.

(2) I did not note the colour of the spores in mass. But as the old gills became yellowish, I fancy the spores must have been yellowish.

(3) I have not Rea's Appendix I at hand, and do not know *constans* or *flava*. But I will look up the description when I have an opportunity.

(4) The *flesh* turned somewhat *rufous* when wounded.

I shall be glad to hear what is the result of the controversy.

Yours sincerely,

W. B. Grove.

The original account in the *Midland Naturalist* reads:

"This species resembles *Russula ochroleuca* and might by some be considered only a strongly marked variety of that, but it differs in other points than colour so remarkably that, in my opinion, it is fairly entitled to be considered distinct. It has occurred for many years successively at Wyndley Pool, Sutton, and always presents the same appearance. In stature it approaches *R. citrina*, but resembles *R. ochroleuca* in the ultimately rugose and cinereous stem, which is at first white and smooth, but ultimately becomes even more dark and

cinereous than in that species. The colour of the pileus is a pure rich chrome-yellow, even approaching the paler shades of egg-yellow, and the same tint is found occasionally on the base of the stem. The gills differ from both the species mentioned in becoming a pale lemon-yellow. The flesh, wherever wounded, becomes somewhat rufous.

R. claroflava

"Pileus 2–3 in., convex, at first bullate, then plane, slightly depressed in the centre, chrome-yellow; margin turned down, at length patent, perfectly even or slightly striate when old, often paler than the disc, but sometimes of a deeper colour; cuticle not so easily separable as in *ochroleuca*; flesh white, yellow beneath the cuticle; stem $1\frac{1}{2}$–$2\frac{1}{2}$ inch × $\frac{1}{2}$–$\frac{3}{4}$, smooth, white, cylindrical, blunt at base, slightly spongy within, at length rugose and cinereous or even blackish; gills scarcely crowded, not reaching the stem so much as in *ochroleuca*, not united behind, white, then altogether pale lemon-yellow, at length subochraceous.

"Among grass in damp places, Wyndley Pool, Sutton Coldfield."

The revised diagnosis in the *Journal of Botany* (1920) 249, reads:

"*Russula claroflava* mihi. Pileus 5–10 cm., across, firm, convex, then depressed, margin even or faintly striate, turned down even when old, deep chrome-yellow, paler on the margin, stained here and there (where abraded) with a rufous tinge; flesh yellow beneath the cuticle. Stipe 5–6 × $2\frac{1}{2}$ cm., white spongy within, somewhat granular, occasionally stained with pale chrome-yellow patches when young, rugose exactly as in ochroleuca and ultimately becoming covered with dark cinereous streaks as in that species. Gills rather thick, straight, not forked, but often joined in pairs near the stem, obtuse and broad in front, narrowed behind, adnexed, altogether tinged with pale yellow, then becoming pale subochraceous; cystidia elliptic-lanceolate, not much projecting. Spores globose, echinulate, 8–9 μ diam.

"On grassy ground among trees on the margin of sphagnum bogs. Flesh of pileus firm, but cheesy; smell faint but not unpleasant; taste becoming unpleasant, but not acrid, with age; colour of pileus rich, pure, and bright."

From the above it would seem clear that the species in question is the same as *R. decolorans* var. *constans Karst.* 1889 (sensu Rea) and *R. flava* Romell 1895. By way of further confirmation Mr Grove was able to name his species in the field at the Norwich meeting of the British Mycological Society. We were fortunate in having him with us on the 3 October 1934, when we explored Westwick and North Walsham Woods. Though late in the season, specimens were gathered and identified by Mr Grove. By the rules of priority we are bound to accept the name *R. claroflava* Grove, which was published in 1888.

Rea has given an excellent short description of the species in his first Appendix to *British Basidiomycetae* in the *Trans. Mycol. Soc.* XII, 218, under the name *R. constans* (Karst.) Romell.

The spores are described differently by various authors. Grove (1920) says "globose, echinulate" 8–9 μ diam. Rea gives 9–12 × 7–9 μ "verrucose". Konrad & Maublanc in *Icones Selectae Fungorum*, pl. 359, give 8–11 × 7–8 μ "nettement verruqueuses-échinulées". J. Schaeffer in his *Russula-Monographie* 8–10 × 7–8 μ sometimes as long as 12 μ "rund bis länglich, punktiert bis dünnstachelig, Stacheln selten über $\frac{1}{2}$ μ nur vereinzelt und sehr fein verlängertverbunden fast isoliert". Crawshay in his *Spore ornamentation of the Russulas* gives average measurement 10 × 11 μ (largest ones 11 × 13 μ). My own measurements show an average of $9\frac{1}{2} \times 7\frac{1}{2}$ μ with some smaller and larger, and the ornamentation exactly agrees with Crawshay whose figures of spores are unsurpassed and who describes the spores as follows: "The surface is covered with a very conspicuous ornamentation, composed of protuberances of various shapes and sizes (often very large) many of which are interconnected by ridges."

The spores are therefore very variable, but the marking on the surface of *Russula* spores can be seen only with a high magnifying power, preferably about 1500 diameters. The cystidia on the gill edge are abundant and turn blue with sulphovanillin.

R. claroflava Grove is a common species usually found in the late summer or early autumn, in wet places under birches.

Russula Turci Bres., *Fungi Trident*, p. 22, pl. XXVI (1881); *sec* Maire, Schaeffer; *non* Singer.
R. amethystina Quél., *Ass. Fr. Avanc. Sci.* p. 5, tab. 4, fig. 13 (1897).
R. punctata Kromb., *Naturget. Ab. u. Beschreib. ess. Schad. u. verd. Schwämm.* IX, p. 13, tab. 66, 20–23 (1845); *sec* Singer, *New Russ.* p. 242.

Pileus 3–7 cm., semi-orbicular at first, then flat with depressed centre, fairly firm when young, fragile later, viscid then dry, granular, the mat surface having the appearance of being very lightly powdered when dry, especially towards margin, often with pock marks and cracks, purple-violet, darker, sometimes black in centre (violet carmine and burnt lake of Ridgway) or with a brown tinge (the range of colour said to include shades of lilac, amethyst, rose) occasionally paler near edge, turning golden yellow when old; margin straight or slightly undulate, not striate when young usually, but may be tubercular when old; cuticle peeling completely off when dry; flesh white, pale violet under cuticle. *Gills* subdistant, cream then ochre, rounded near margin, narrowed towards stem, free, thick with sharp straight edge, broad, often forked, veined. *Stem* 5–7 cm. very variable in shape, either thicker or attenuated at base, 1–$2\frac{1}{2}$ cm. thick, spongy, fragile,

white sometimes with a red tinge; flesh white. *Spores* in mass, ochre, G of Crawshay's chart, broadly ovate 8–10 × 7–8 μ. with prominent warts and reticulations. *Basidia* 40–50 × 8–12 μ. *Cystidia* on edge and face of gills lanceolate with long sharp point, no blue reaction with sulphovanillin; none on pileus. *Taste mild. Smell* none, except at base of stem which usually smells of iodoform, probably on account of the attached mycelium which has the iodoform odour.

Chemical reaction with ferrous sulphate: light pink.

Habitat: under pine trees. New Forest, Hampshire, under pines among bracken 21 and 27 September 1935; Sheffield Park, Sussex, under alien conifer, 5 October 1935.

There has been some discussion about the name to be applied to this species. Bresadola does not mention the characteristic smell, but this could easily be overlooked. Specimens sent by Maire to Bresadola were named *R. Turci*, and three dried specimens in the herbarium of Bresadola examined by J. Schaeffer were also found to be this species. That would seem conclusive, but Rolf Singer states that Bresadola wrote to him that "*R. Turci Bres. n'est pas Turci Maire*". Singer claims that Bresadola named for him another species as *R. Turci*, which had cystidia on the pileus, and which Singer considers to be identical with *R. lateritia* Quél. (1885) and that therefore this species should bear the name *R. Turci* (1881).

To avoid confusion J. Schaeffer adopts the specific epithet *amethystina* Quél. which is also the name under which Crawshay had described this species. (The *R. Turci* in Crawshay's book is another species.)

R. Singer adopts *R. punctata* Krombholz.

What name are we to adopt?

The discussion centres round the microscopic character of the pileus which Bresadola never defined. It is practically certain that he himself confused two species. We are not greatly helped by his *Iconographia Mycologica*. The volumes containing the *Russula* plates were published after his death. Pl. 463, with the title *R. Turci* Bres., depicts a *Russula* which closely corresponds to our species. Pl. 467, called *R. amethystina* Quél., depicts a *Russula* with an umbonate pileus and probably is the same as *R. caerulea* Cooke. Pl. 453 is *R. aurata*, but *R. lateritia* Quél. is given as a synonym, so it is clear Bresadola did not consider there was any connexion there, if the details in the *Iconographia* were supplied by him, as we are entitled to assume.

The name *R. Turci* Bres. must either be relegated to the lumber heap or we must accept Maire's view which held the field before Singer brought about this intolerable confusion.

Another way out has been proposed by Maire in *Bull. Soc. Mycol. Fr.* XXVI (1910), 174. He points out that the description of *R. nauseosa* Pers. in the *Monographia Hymenomycetum Sueciae* is near enough to justify this name being adopted for our species. *R. nauseosa*

sensu Bresadola has no smell, but the *nauseosa* of Fries is stated to be mild, but with smell often "nauseosus". That is so with *R. Turci*. If we follow Maire, the synonymy will be as follows:

Russula nauseosa (Pers.) Fr. *sec.* Maire
Russula Turci Bres. *sensu* Maire *non* Singer
Russula amethystina Quél.
Russula abietina Peck
Russula nauseosa Bres.

Russula Velenovskyi Melzer & Zvara (*Ceské Holubinky*, 1937).

Pileus 3–8 cm., at first convex, then flattened and depressed in centre, light brick-red (Dragon's Blood Red of Ridgway) rather darker in centre, mat granulate surface, cuticle often cracked near margin. *Gills* cream then pale ochraceous, attenuated near stem, rounded in front, minutely emarginate, free, sometimes forked at base, all one length, crowded. *Stem* 6 cm. in largest specimens, 4 cm. in smaller, cylindrical, or thickened at base, white, or partly flushed with pink, often with parallel lines, spongy but not fragile. Spores in mass, pale yellow-ochre (E to F of Crawshay's spore deposit chart). *Spores* oval, warted, apiculate, $8–9 \times 6–7\frac{1}{2}\,\mu$, no visible reticulations. *Cystidia* abundant, mostly blunt, on edge of gills, $45–50 \times 7–10\,\mu$ mostly with thread-like appendage, either short or long, turning blue with sulphovanillin; no cystidia on pileus in our specimens, but long worm-like septate cells $3–5\,\mu$ diam, with swollen ends turning blue with sulphovanillin. Schaeffer states that in young specimens cystidia may sometimes be seen on the pileus $40–60 \times 7\,\mu$. *Flesh* white, unchanging, pink under cuticle. *Smell* none. *Taste* mild (or slightly bitter at first, sec. Melzer & Zvara).

Reaction to ferrous sulphate, pink; reaction to phenol, reddish brown.

Habitat: in deciduous and coniferous woods. Epping Forest, Essex, October 1933, under beeches. There were many specimens, all cracked round the margin, even when just appearing above the ground. Broadwater Forest, Sussex, October 1934, September 1935, under larch, near birches. A few specimens, only one of which showed signs of cracking near the margin.

This may very well be *R. cutifracta* in the sense of Rea (British Basidiomycetae) and Peltereau (*Bull. Soc. Mycol. Fr.* XXIV (1908), 105), but in Cooke's original description "*R. cutefracta*" is a very robust species with a purple or greenish pileus and white gills and presumably white spores, though the colour of the spore mass is not definitely stated. Russulas with gills at first white and then yellow when the spores develop are well-known and we can assume that this would have been mentioned by Cooke.

The cracking of the periphery in species of *Russula* is not uncommon,

the best known example being *R. virescens* which consistently shows a pileus broken up into areolae. This phenomenon may occasionally be observed in other species, notably in *R. vesca* where the gills often grow a little beyond the edge of the periphery and sometimes cause the cuticle of the pileus to crack. Doubtless the same thing happens with other species. Most continental mycologists consider that *R. cutefracta* of Cooke is a form of *R. cyanoxantha* and the colours of Cooke's figures in his *Illustrations of British Fungi* certainly suggest this.

Russula farinipes Romell in Britzelmayr's *Hymenomycets Südbayern* (1893).

(*R. subfoetens* W. G. Smith *sensu* Maire and Melzer & Zvara; *non* Rea.)

Pileus 3–5 cm., more or less flat, depressed in centre, then turning up at edge, transparent when held up to light, shallow, firm, elastic; cuticle closely adnate, not peeling even at the edge; somewhat viscid at first, soon dry, sometimes with cracks showing white flesh underneath, light straw- or ivory-colour with rusty brown spots, somewhat mealy under a lens; margin incurved at first, edge regular or undulate, striate then sulcate, but not coarsely tuberculate; flesh white. *Gills* crowded, adnate or subdecurrent, often weeping when young, pointed at both ends, elastic, thin, almost white at first, pale later, edge straight, all one size usually, sometimes with a few shorter ones, veined at base when old, somewhat elastic. *Stem* 3–4 cm., cylindrical or attenuated at the base, firm, elastic, solid then spongy, smooth or often mealy, white, often with rusty patches, flesh white. *Spores* in mass, white, globose or subglobose, 6–8 × 6–7 μ, with shallow isolated warts occasionally joined up with faint anastomosing lines. *Cystidia* abundant on edge and face of gills, also on pileus and stem, all lanceolate, sharply pointed, turning blue with sulphovanillin, 60–120 × 6–8 μ. *Cystidia* in bundles on stem, 40–60 × 8–10 μ, producing the mealy surface to which Romell's name refers. No smell. *Taste* peppery.

Habitat in deciduous woods. Not uncommon.

The above description is from specimens gathered in damp woods, Frant Bottom, Sussex, August 1934, under birches, near oaks and beeches. Mayfield, 12 August 1936.

When authorities like Maire, Melzer and Zvara, and others identify this species with *R. subfoetens*, it is chiefly because Cooke in his *Illustrations*, Pl. 1016 (1047) characterized "the whole plant tough and elastic", a feature rarely met with in the genus *Russula*. The species described above is both tough and elastic, but the spores are white, not pale ochre as given by Smith, and it has very little smell (if any). Mr Carleton Rea informs me that he considers *R. subfoetens*

to be a different species, I therefore adopt *R. farinipes* which is a much better name.

R. simillima Peck has also been regarded as this species, but until American species have been studied on the spot by mycologists fully acquainted with European species, it seems better to leave them out of our synonomy.

Melzer has given an excellent figure of this species in *Bull. Soc. Mycol. Fr.* XLVIII, pl. XXIV, under the name *Russula subfoetens* Sm.

At the British Museum there are many original paintings named *Russula subfoetens* by W. G. Smith but representing various species. The only one that almost certainly corresponds to the species described above is that by Edwin Wheeler dated 1891 (the upper one).

Russula laurocerasi Melzer *Casop. es. houb.* (1920); in *Bull. Soc. Mycol. Fr.* XLVIII (1932), pl. XXIV B (1932).

This *Russula* is in most respects like *R. foetens* (Pers.) Fr. though normally smaller and more compact. The smell is less rancid, like burnt almonds. The only feature that clearly distinguishes it is the ornamentation of the globose spores which have deep ridges, and are a remarkable sight under the microscope; sometimes the ridges go right round the spore. Size 10–14 μ.

I have only come across *R. laurocerasi* once, at Frant Bottom, August 1934, but it may be fairly common. Melzer has indicated Cooke's plate 1016 (1047) for this species, and my specimens corresponded closely to these drawings. Cooke's plate has the name *Russula subfoetens* Smith, but the drawing is by Massee. The original drawing made in 1873 by W. G. Smith of *R. subfoetens* in the British Museum is very different and looks more like *R. fellea.*

Russula solaris Ferd. & Winge in *Meddelelser fra. For. til Svampek* (1924).

Pileus 2–6 cm., convex, thin, very fragile, viscid, at first smooth, glabrous, cuticle peeling nearly to centre, bright chrome-yellow (yolk of egg) occasionally with an orange tinge, paler near the margin which is incurved and smooth at first, finally striate-tuberculate; flesh white. *Gills* subdistant, variable in shape and width, adnate, rounded near margin of pileus, thin, edge straight, at first white then straw-colour, often forking from near stem. *Stem* 2–5 cm. long, 8–20 mm. diam., usually attenuated above, soft, spongy, white, rarely with lemon spots, sometimes curved; flesh white. *Spores* in mass, cream, C of Crawshay's chart, subglobose or ovate, 7–9 × 7–8 μ, with prominent isolated warts. *Cystidia* on gill abundant, less so on face, blunt or sometimes pointed, turning blue with long narrow cells in cuticle of pileus turning blue in sulphovanillin 2–3 μ wide. *Taste* acrid. *Smell* none, but Lange says "odour like mustard oil", and J. Schaeffer: smell faint of mustard sauce (*Senfsauce*).

Chemical reactions of flesh: ferrous sulphate, pink; phenol, no reactions at first, then pinkish brown.

Habitat: under beech. Buckhurst Park, Sussex, 25 August 1934, 2 August 1936. Probably not uncommon.

Very like *R. lutea*, the spores of which are of a deeper colour, and the taste mild.

Russula exalbicans Secr 1833. Konrad & Maublanc, *Icon. select. fung.* pl. 354, as *R. depallens* subsequently amended to *R. exalbicans*.

Pileus 5–7 cm., semiglobate with incurved margin then plane, finally depressed, with sharp edge, thin except in centre, firm, viscid at first, smooth or granular under a lens, often with a satiny reflexion, cuticle separable half way to centre, blood red or bright pink with pale areas, or completely pale or a dirty white; sometimes a pale pink with a deeper colouring in centre and round margin, which is regular or undulate: margin smooth at first, then striate: flesh white or grey, especially in wet weather. *Gills* crowded, very variable in shape, mostly narrow, almost linear, sometimes round near pileus and narrowed towards stem, thin, brittle; edge straight, smooth; white then cream, very few short gills. *Stem* cylindrical or thickened at base, 3–4 cm. long, 1–1½ cm., thick, firm, spongy inside, rugulose, white then grey, often grey in young specimens; flesh grey when wet, white when dry. *Spores* buff-colour, E to F of Crawshay's chart, oblong, warts prominent, with distinct reticulate marking, 9–12 × 6–7 μ, very variable in size, apiculus prominent. *Cystidia* on edge and face of gills abundant with short filiform appendage, turning blue with sulphovanillin; cuticle of pileus with narrow vermiform cells that colour dark blue with sulphovanillin. *Taste* mild except in gills which are acrid, especially in young specimens; often mild when old, and so easily overlooked. *Smell* none or faintly pleasant.

Chemical reactions of flesh: ferrous sulphate, very faint pink at first, which afterwards nearly disappears; phenol, no reaction at first, then purple.

Habitat: under birches. Broadwater Forest, Sussex, 15 September 1935, 2 August 1936, among grass under birches.

This species is probably common. It has the appearance of *Russula depallens* and has been confused with that species. It is extremely hygrophanous and the greyness of the stem, presumably due to the absorption of moisture, is a very striking feature. The spores are however coloured in the mass.

Russula pseudo-integra Arn. & Gor. in *Bull. Soc. Mycol. Fr.* XXIII (1907), 177, *non* Crawshay.

Pileus normally of medium size, 7–10 cm., sometimes much larger, soft, hemispherical at first then flat, fairly thick, usually scarlet, but sometimes paler especially in centre, turning almost white when old,

viscid then dry, cuticle separating half way to the centre, sometimes completely; flesh reddish under the cuticle; edge not usually striate, but may be tuberculate when old. *Gills* fairly crowded, white at first, then cream and finally ochraceous, attenuated towards stem, more or less round near margin of pileus, wide, thin, edge straight or rather floccose, adnexed almost free, minutely emarginate, usually all of one length, rarely forked and unequal. *Stem* subcylindrical, about 10 cm., long, but often much taller, fairly firm at first, often swollen and rugulose, soon spongy, white. Spore mass ochraceous (G of Crawshay's chart). *Spores* subglobose, $7\frac{1}{2}$–9×7–$8\,\mu$, warted with fine lines between some of the warts. *Cystidia* of gills mostly with filiform appendage and covered with an incrustation which does not reach the apex and dissolves in water; no cystidia on cuticle of pileus. *Flesh* white, mild then bitter (*not* peppery).

Habitat: in deciduous woods, especially oak and birch. Saxonbury Wood near Frant, Sussex, September 1933, August 1934; Gray's Wood near Haslemere, Surrey, September 1932; Epping Forest, 13 October 1934. Several localities in Sussex 1935 and 1936.

This beautiful *Russula* is fairly common in our woods in the summer and early autumn. It is easily recognizable by its brilliant scarlet pileus, cream or ochraceous gills and bitter taste after mastication. When young it looks very like *R. lepida*, which differs in having white gills and a powdery surface of the pileus.

Tricholoma
Inocybeoides
sp.nov.

Mycena
uracea
sp.nov.

STUDIES IN THE GENUS *USTULINA* WITH SPECIAL REFERENCE TO PARASITISM

III. SPORES—GERMINATION AND INFECTION

By W. H. WILKINS

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(With 13 Text-figures)

I. INTRODUCTION

In accounts of the tropical form of *Ustulina* (*U. zonata*), it has often been stated that infection is by spores. Steinmann (1923) states that it is "exclusively by spores", but spores do not seem to be essential, for Petch (1928) asserts that "infection can take place merely *via* contact of lateral roots". Tunstall (1922) states that both methods of infection may occur.

This paper is an investigation into the probability of infection by spores in the temperate form of *Ustulina* (*U. vulgaris*), and it deals mainly with spore germination from the restricted standpoint of parasitism, though some experiments are described which are not directly connected with the parasitic aspect but relate to spore germination in general.

II. PREVIOUS LITERATURE

There seems to be no previous account of spore germination in the genus *Ustulina*. It will serve no useful purpose to introduce here a historical review of the well-known papers on spore germination in general; there is an excellent annotated summary of such literature (on Basidiomycetes), covering the period 1842–1901 by Ferguson (1902), and more recent and pertinent work will be discussed incidentally in the text. A useful paper by Child (1929) deserves special mention, as it appears to be the only account of spore germination in an allied genus; it has, however, an academic rather than an economic outlook.

III. MATERIAL

The material used in this work was collected during three seasons from beech trees in various parts of the country. Fructifications on trees other than beech were invariably insufficient in quantity to be used for experimental purposes. Fructifications were collected once every four weeks, generally at or near the beginning of the month, and

spores from any collection were used for experimental work during the four weeks following their collection. The fructifications were kept in glass dishes in the laboratory at an approximately constant temperature of 15° C. Under these conditions, spores emerged from the perithecia during the first few days and then—there being no further exudation—remained on the surface of the fructification for several months. It was from these superficial spore masses that the spores for experimental work were taken.

Material was first collected in August. Since there was no spore emergence from this, it was presumed that the spores were not mature. This supposition was confirmed to some extent by the next collection in September, for, in this, though there was some exudation of spores, many of these were immature and germination was poor. Experimental work was not started till the beginning of October. Spores exuded vigorously in the laboratory, from material collected during the months of October and November, and they exuded to some considerable extent from collections made during December. From January and February collections, however, there was comparatively little exudation, and in March there were only one or two drops from the whole of the material collected.

IV. METHOD

As there is a certain consistency of method—at any rate as far as the "hanging-drop" technique is concerned—it will be described here in detail to avoid unnecessary repetition.

In almost all experiments, spores from different perithecia were taken from the "blobs" on the surface of the fructification and were stirred with a sterile needle into a sterile germination medium so as to ensure a thorough mixing and separation of the spores. In the meantime the required number of ring cells had been kept at the temperature subsequently to be used for incubation, each having at the bottom a few drops of the liquid to be used in the drop. This liquid preserved the equilibrium of vapour pressure, and the previous incubation tended to prevent undue condensation of moisture on the cover-slip and consequent spreading and dilution of the drop. After the mixing of the spores, a ring cell was taken from the incubator, a loop of the spore suspension was put on to a cover-slip which was then inverted on to the slightly vaselined edge of the ring cell. The ring cell was then immediately returned to the incubator.

In most of the experiments the average percentage germination has been taken as the basis of comparison or the criterion of successful germination, because, though in complete agreement with Tomkins (1932) as to the undesirability of taking this as the sole criterion, it is suggested that the experiments dealing with the latent period, rate

of elongation of germ tube and actual lengths of germ tubes have shown that percentage germination alone usually gives an adequate idea of the relative values required.

Almost all previous workers have commented on the erratic nature of spore germination. Ferguson (1902, p. 23) refers to this and says for example that one culture out of four duplicates gave 90 % germination while the other three gave absolutely none; no explanation could be given of these variations. Child (1929, p. 416) states that all cultures were made in duplicate or triplicate and that the frequent erratic results necessitated repetition as many as ten times. Webb (1921, p. 296) is less emphatic in his comments but says that unexplainable fluctuations sometimes occurred. In view of my own experience all the above comments are fully justified. An attempt, however, has been made to reduce these erratic variations which seemed to be attributable to two main factors:

(1) Insufficient consideration of the physiological condition of the spores.

(2) Carrying out experiments on a scale which was not sufficiently large to reduce the probable error.

With the object of reducing erratic results to the minimum the following technique was adopted:

(*a*) The physiological condition of the spores in terms of "age" was always allowed for (see p. 50). Spores of the same age were used in any one experiment, and when part of an experiment failed the whole experiment was repeated.

(*b*) In the "hanging-drop" experiments, six fields were counted at random in each of the four drops. This was done in triplicate.

(*c*) Results were estimated on the average of the three, and each "average percentage" total in a table, or each point on a graph, represents a count of approximately a thousand spores.

(*d*) Ring cells were put into the incubator on wooden racks and never directly on the floor of the incubator. This prevented the condensation of moisture.

(*e*) Immature (hyaline) spores were not included in the counts.

(*f*) Glassware was kept scrupulously clean.

It was found that the concentration of the spores in the drop did not materially affect germination, and that vaseline did not appear to have a deleterious effect.

Though, in spite of these precautions, erratic results did occur, these could usually be traced to accidents, and it was felt that, on the whole, results were consistent within the limits of normal deviation.

It was known that spores of different ages did not give the same percentage germination (details later). It is therefore obvious that in experimental work, comparison is difficult if not impossible unless the age of the spores is taken into account. To determine whether there

was any appreciable falling off in germination-capacity during the four-week experimental period following each collection, spores were germinated in tap-water extract of beech at the beginning, middle, and end of each of these periods, and from these results it was possible to estimate the "expectancy of germination" in similar media with considerable accuracy. Even when using different media, comparison of results was facilitated. These records are shown in Fig. 1.

Fig. 1 is a key to the percentage germination which might be expected from spores of any given age. The age of the spores is stated for each experiment, in the form of symbols. The symbol N 4/8, for

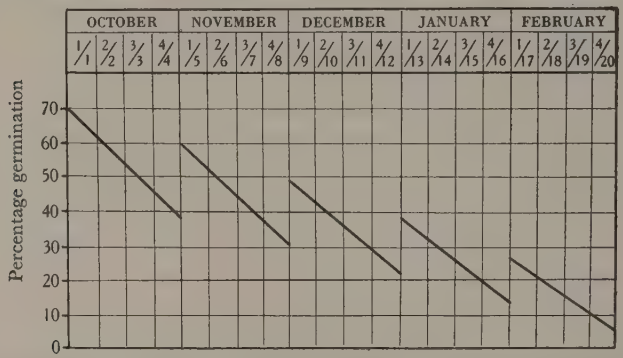

Fig. 1. Approximate percentage germination expected in relation to the age of the spore.

instance, means that the spores were those collected near the beginning of November, that they were used in an experiment which was started in the fourth week from their collection, and that their "age", dating from the beginning of the season, was eight weeks. Reference to the figure shows that the percentage germination to be expected (in tap-water extract of beech) was about 30–40 %.

This experiment was carried out during the season 1934–5, but though the work on spore germination continued during the following season this control experiment was not repeated. Frequent checks showed that the state of affairs was essentially the same in the second season as in the first. As an example the percentage germination of the first collection of spores in October 1934 was 72·32, while that of the first collection in October was 73·65.

V. THE FRUCTIFICATIONS

Fructifications appear as black, charcoal-like crusts with an irregularly rugose surface minutely dotted with the ostioles of the perithecia. Each fructification may be several centimetres in diameter, but as adjacent fructifications become confluent, the whole mass may

cover an area of a square foot or more. On beech trunks they are usually found at the base, often in crevices or hollows, or intermittently scattered along the sides of the surface roots. They seem able to exist on the surface of the bark but are often found beneath it, and the bark can then be easily pulled away to expose them. Fructifications may also be found spread over the dead and exposed wood of wounds on any part of the trunk or branches or on rotten wood on the inside of hollow trunks. Being carbonaceous in substance they may persist for many years after they have ceased to function. They are often found on living stumps but are rarely present—in a functional condition—on dead wood. Presence of fructifications is usually an indication of disease. To what extent this is an invariable sign is unknown, as it is obviously impossible to fell trees to find out and I have not yet had the opportunity of being present at the felling of a previously examined area. On the other hand, there may be disease where no fructifications are apparent.

VI. SPORES—SHAPE AND SIZE

There are eight spores in an ascus, arranged in an irregularly oblique series as shown in Fig. 2, diagrams 1 and 2.

Saccardo (1882) describes the spores as follows: "Sporidiis oblique monostichis, fusiformibus inaequilateralibus, immo curvalis, nigricantibus." There is, however, considerable variation in shape; some of the commoner types are shown in Fig. 2, diagrams 3–9. In mass, the spores are black, but under the microscope they may appear black, dark brown, red-brown, dark greenish with a darker oval centre, pale green or almost hyaline. The first four kinds are capable of germination, but the last two—presumably immature—have not been known to germinate. Each spore is surrounded by a hyaline exospore.

Spore size is an important feature of systematic determination; consequently the average size was estimated by measuring some five hundred spores all collected from fructifications growing on beech.

In the first place the lengths and breadths of 218 spores were measured. The spores were stirred into a drop of distilled water on a slide, allowed to dry into a film at laboratory temperature and then measured directly by means of a $\frac{1}{12}$ in. oil immersion objective and a micrometer eyepiece. The variation in size is considerable; the lengths were found to vary from 36·0 to 24·75 μ, the breadths from 6·0 to 8·25 μ. In spite of this variation, the standard deviation of the mean, calculated by the usual formula $\sigma = \sqrt{\frac{\Sigma (v_x)^2}{n^2}}$, was significantly small, and the average size of the 218 spores was found to be

$$30{\cdot}59 \pm 0{\cdot}13 \times 7{\cdot}28 \pm 0{\cdot}05\,\mu.$$

The standard deviation of a single observation was: for the lengths $\pm 1{\cdot}99\,\mu$, and for the breadths $\pm 0{\cdot}72\,\mu$.

It is interesting to compare these measurements with those of certain other investigators for (presumably) the temperate form of *Ustulina*, e.g.:

Tulasne	1863	$32\text{–}25 \times 6{\cdot}5\text{–}\ 8{\cdot}0\,\mu$
Saccardo	1882	$40\text{–}32 \times 8{\cdot}0\text{–}10{\cdot}0\,\mu$
Winter	1887	$40\text{–}32 \times 8{\cdot}0\text{–}10{\cdot}0\,\mu$
Traverso	1906	$43\text{–}28 \times 7{\cdot}0\text{–}10{\cdot}0\,\mu$
Van Overeem	1924	$40\text{–}28 \times 7{\cdot}0\text{–}10{\cdot}0\,\mu$
Miller	1930	$34\text{–}28 \times 7{\cdot}0\text{–}10{\cdot}0\,\mu$

The measurements in the list vary considerably with the individual observer, but, in general, the sizes given are rather larger than I have found. In the list the whole range is greater and, if it can be assumed that the error frequency is distributed according to the normal curve, then the average size can be estimated as approximately $33{\cdot}0 \times 8{\cdot}5\,\mu$, which is higher than the average size obtained in the experiment. The spore size as given by Tulasne is the closest approximation to the sizes found in this work, for though the length as given by Miller is very close, there is disagreement in breadth, and the measurements of the other investigators give a much higher average than I ever obtained.

This discrepancy in results may be due to variation in spore size in different "strains" of the fungus or may be due to personal error in measurement. In order to test the personal factor and to verify the previous results, spores, which in order to include as wide a range as possible, had been collected at various times during the spore season and from different districts, were mixed indiscriminately and measured. One hundred were measured by each of three research workers in the laboratory. Each was provided with spores and left independently to work out the sizes, by the previously described method. The results are given in Table I.

Table I. *Measurements of spores by three research workers*

	Range		
	Length	Breadth	Average size
	μ	μ	μ
A	39·00–25·50	6·00–11·25	$30{\cdot}41 \pm 0{\cdot}28 \times 7{\cdot}53 \pm 0{\cdot}10$
B	44·00–25·50	6·00–10·50	$31{\cdot}30 \pm 0{\cdot}27 \times 7{\cdot}58 \pm 0{\cdot}07$
C	39·26–25·67	6·04–9·81	$31{\cdot}14 \pm 0{\cdot}29 \times 7{\cdot}87 \pm 0{\cdot}07$

Table I shows that the three results agree closely. There is little difference between the average size of these 300 spores and that of the 218 spores measured previously. This suggests that the personal

factor can be regarded as negligible and, assuming the measurements of the previously listed workers to have been correct, postulates a greater variation in the size of spores of *Ustulina* than has been encountered in the present investigation.

The "z test" of Fisher (1932) was applied to the results shown in Table I. When $n = 300$, the 5 % value of z as given by Fisher's table (p. 224) is approximately 0·55. The value of z for spore lengths is 0·45 and for breadths 0·82, indicating that whereas the lengths can be regarded as belonging to the same population the breadths cannot. This discrepancy is probably due not so much to a personal error of measurement, however, as to a slight inaccuracy of microscope calibration on the part of research worker C.*

The average size of the whole 518 spores was then calculated and found to be

$$30{\cdot}82 \pm 0{\cdot}11 \times 7{\cdot}47 \pm 0{\cdot}03\,\mu.$$

The standard deviation of a single observation works out at $\pm 2{\cdot}54\,\mu$ for the lengths and $\pm 0{\cdot}68\,\mu$ for the breadths. That is, the size of the spores of *U. vulgaris*, within the limits of this experiment, can be expressed as approximately $31 \times 7{\cdot}5\,\mu$.

VII. DETERMINATION OF A MEDIUM FAVOURABLE FOR GERMINATION

A preliminary trial having shown that 25° C. was a suitable temperature for germination, spores were set up in ring cells containing respectively distilled, tap, and rain water as well as six different water extracts of beech wood. The extracts were made by soaking 10 g. of wood shavings in 100 ml. of the appropriate liquid for 24 hr., filtering and autoclaving. The *p*H of these solutions was taken immediately before use. Five to eight ring cells were set up with each solution and these were incubated at 25° C. for 48 hr. Random fields were then counted, the percentage germination calculated, and the characteristics of the germ-tube growth noted.

In most work on spore germination, nutrient media are commonly used. Tomkins (1932, p. 418) recommends the use of nutrient solutions rather than water, on the grounds that the germination rate is higher and the results more consistent. Ferguson (1902, p. 14) remarks that nutrient media certainly enhance the germination of the spores of *Psaliota campestris*. From the standpoint of infection, however, nutrient media are of less significance, and the work on the influence of the "infection drop" on spore germination by Brown (1916) suggested that the water extracts satisfied the nutrient requirements

* My thanks are due to Dr Clapham, of the Oxford Department of Botany, for kindly confirming the results of the statistical treatment.

and gave conditions approximating to those obtaining in nature. To facilitate comparison with the results of other workers, germination in nutrient media is dealt with later in the paper.

The results are shown in Table II:

Table II. *Germination in water and various wood extracts*

		Age of spores: O 1/1				
	*p*H	No. exam.	No. germ.	%	Av. %	Germ tubes
Distilled water	6·8	478	220	46·03	46·66	Straight, about 1 per spore. Av. length 15·2 μ.
		488	232	47·54		
		431	200	46·40		
Rain water	6·9	400	56	14·00	13·34	Straight, 1–2 per spore. Av. length about 20 μ.
		312	44	14·10		
		285	34	11·93		
Tap water	7·2	570	325	57·02	59·41	Straight, usually single. Av. length 90–100 μ.
		431	286	66·36		
		454	249	54·85		
Distilled water extract of beech wood	6·4	540	321	59·44	55·09	Straight, not more than 2 per spore. Av. length 74 μ.
		231	107	46·32		
		499	297	59·52		
Rain-water extract of beech wood	6·6	388	122	31·44	34·82	Very twisted but not branched, 2–3 per spore. Av. length 65 μ.
		321	108	33·64		
		396	156	39·39		
Tap-water extract of beech wood	6·8	338	240	71·01	71·62	Straight, usually single. Av. length 90–100 μ.
		339	238	70·21		
		353	260	73·65		
Tap-water extract of beech bark	6·8	491	267	54·38	53·02	Branched, short, and very numerous. Av. length about 8 μ.
		532	271	50·94		
		593	319	53·79		
Natural rain-water collected from the tree roots	8·8	454	196	43·15	42·10	Straight and unbranched, 1–2 per spore. Av. length 30 μ.
		508	209	41·14		
		438	184	42·01		
Tap-water extract of diseased wood (*Armillaria mellea*)	4·4	631	43	6·81	7·41	Very branched, very short and several per spore.
		512	45	8·79		
		550	32	5·82		

Table II illustrates the method of calculating the experimental results. In subsequent tables the results will be expressed in terms of the average percentage germination.

The results in the table indicate that the germination medium which gave the highest percentage germination and the longest germ tubes was tap-water extract of beech wood, though several of the other media were almost as good. The tap-water extract was subsequently used in most of the experimental work. The rather better germination in tap-water as compared with distilled water is the exact reverse of the state of affairs found by Ferguson (1902) or Mounce (1929). Germination in rain-water is not so good. This has some significance, as both rain-water and its corresponding extract are probably the most important germination solutions in nature. The so-called "natural rain-water", which was water collected from the hollows among the roots and at the base of the trunk and which is regarded as a very probable means whereby infection might occur in

nature, gave good germination. The comparatively good germination in tap-water extract of bark rather supports the idea that spore germination and subsequent mycelial growth can take place on the outside of the bark even when there is no wound exposing the inner tissues. In tap-water extract of wood attacked by *Armillaria mellea*, germination was very poor. This suggests that *Ustulina* would find difficulty in following *Armillaria* as a secondary infection.

VIII. GERMINATION

(*a*) Early stages in germination

Age of spores: N 1/5

In this experiment the spores were germinated in tap-water and incubated at 25° C., and though there is some variation the general course of the process is as follows:

The first sign of germination is the swelling of the ventral side of the spore (Fig. 2, diagram 10). This is usually apparent about 8–12 hr. after the spore was first put into the germination medium, but sometimes there is no swelling at all. After about 10–24 hr.—this is very variable—when the width of the spore has increased by about 50 or even 100 per cent, the spore coat splits down the ventral side. The first germ tube then appears (Fig. 2, diagram 11), either from the centre or, quite often, from one side of the median swelling. If there are two tubes they usually grow out one on each side of the middle (Fig. 2, diagram 12) and, rarely, the contents come out of the spore wall along its whole length (Fig. 2, diagram 13), but even so, later growth is always more rapid at one or more of the points previously mentioned (Fig. 2, diagram 14). Quite commonly there are three germ tubes from one spore (Fig. 2, diagram 15); there may be as many as five (Fig. 2, diagram 16), but more than this have not been seen. The germ tubes are typically 4 μ in width throughout their whole length, except that at the point where they leave the spore they may be slightly wider and at the distal end they are often slightly narrower.

(*b*) Rate of elongation of the germ hypha

Age of spores: N 2/6

Here also tap-water was used as a germination medium because this had been shown to give the straightest, and usually, single germ tubes. The drops were incubated at 25° C. and the spores were examined at intervals for the first sign of germ tube emergence; germination was then considered to have taken place. The latent period was noted and the subsequent growth of the germ tube was measured every hour for 12 hr. or until growth ceased. By setting

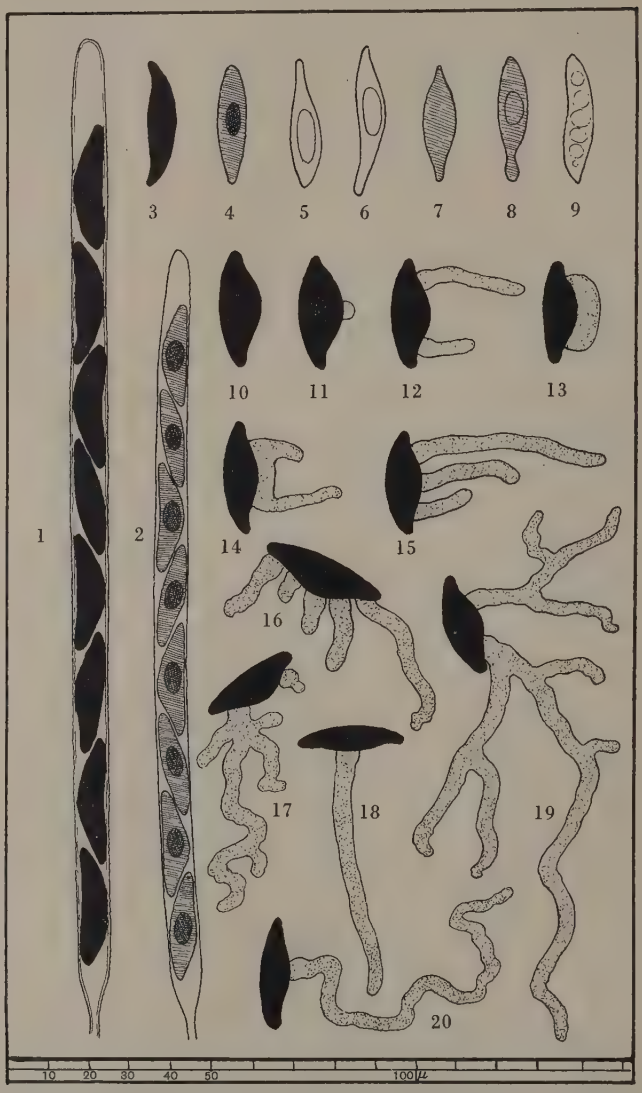

Fig. 2. Spores—size, shapes and types of germination. Diagrams 1–2, showing spores in asci; 3–9, examples of various shapes of spores; 10–20, stages in different types of germination.

up one set of spores in the morning and another at night and fitting together similar rates of growth, it was possible to obtain representative measurements of germ tubes over a period of 24 hr.; after that time measurement became unreliable or impossible.

In connexion with this experiment it is necessary to emphasize the erratic nature of the germination and the inconsistencies of the growing hypha. The latent period is extremely variable. Some spores germinate after 9 hr. incubation and others, apparently mature and in the same drop, do not germinate at all. The rate of elongation is equally irregular, as some germ tubes may be described as fast growers, others as slow growers. A germ tube may grow consistently well for a time and then either slow down and stop, or it may stop quite abruptly, or a germ tube which has grown very slowly for a time will suddenly start to grow rapidly. It is not uncommon for a germ tube which has stopped growing for a considerable period to start again and grow vigorously. Even those germ tubes which are regarded as showing a reasonably consistent rate of elongation do not grow at a uniform rate throughout the whole period of growth, and the growth rate for any one hypha in different hours may vary from 0 to 54 μ.

The erratic nature of germ tube elongation has been noted by Henderson Smith (1924, p. 66).

Under these circumstances it was essential to measure a very large number of germ tubes; the records were then fitted together, and eventually the total was reduced to twenty hyphae which were considered to be representative of varying types of growth. The complete table is not given, but in Fig. 3 are plotted the growth increment curves of:

(1) A single hypha whose rate of growth was faster than the average; this is referred to as a "fast grower".

(2) A single hypha whose rate of growth was slower than the average; this is referred to as a "slow grower".

(3) The average of the twenty hyphae.

It is evident that, with the exception of the fast grower, of which the upper limit of growth was not reached, the growth is represented by a sigmoid curve. After the latent period, which averages about 17 hr., there is an initial growth period of about 6 hr., when growth is slow—not more than about 2 μ per hour—but which is approximately the same for all whatever the subsequent variation in rate may be. This is followed by the main period of growth where there is considerable variation in relation to the time axis though the type of curve remains the same. Over the whole of this period the rate of growth varies from approximately 4·7 μ per hour in the slow grower, to approximately 16·7 μ per hour in the fast grower, the average rate of the twenty being about 8·6 μ per hour. The third period is the slowing up of the growth rate due to conditions obtaining in the drop

and is indicated in the graph by the gradual approximation of the curve to a horizontal line.

As branched germ tubes—which are rare in tap-water—were not

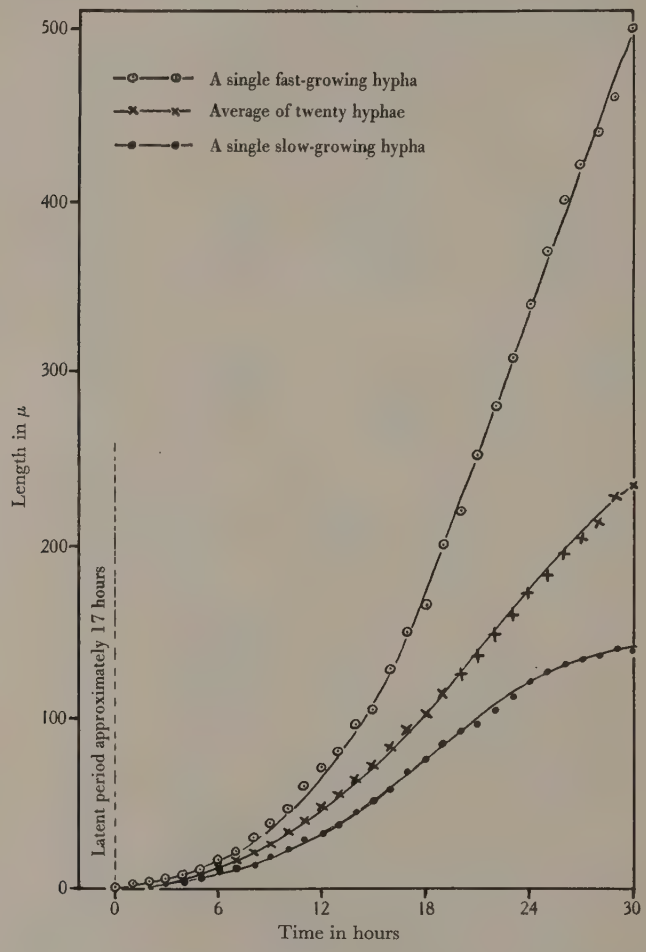

Fig. 3. Hourly increment of growth of germ-hypha plotted against time.

included, and as the germ tubes maintained a uniform diameter throughout the period of observation, the growth rate of these hyphae can be expressed in terms of direct increment in length.

It is interesting to compare these results with those of Henderson

Smith (1924). He worked with a branching hypha and measured the total growth of the main axis plus the growth of each of the branches at various time intervals. When the logarithm of the length of the main axis alone was plotted against time he obtained a line which was

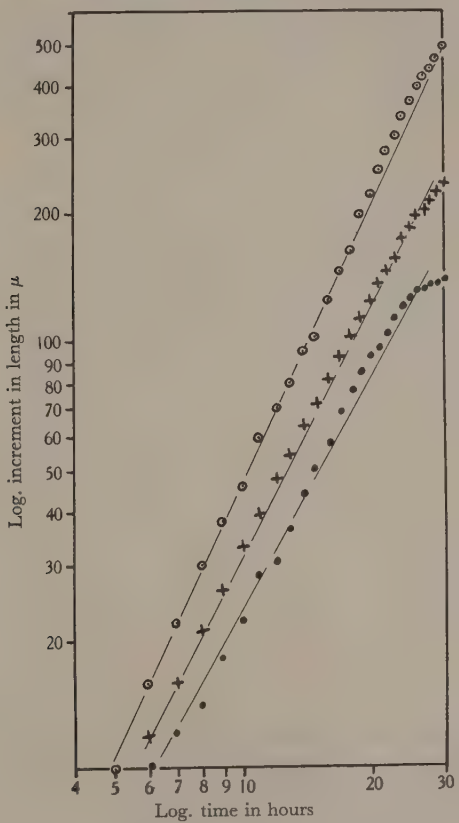

Fig. 4. The logs. of the hourly increment of growth of this germ hypha plotted against log. time

concave to the time axis, but when the logarithm of the length of the main axis plus the lengths of the branches was so plotted he obtained a straight line, i.e. the growth could be described as logarithmic, the equation being of the $y = ak^t$ type. The total increment was constantly proportional to the total length and the relative growth rate was approximately constant.

The early growth rate of the germ tube of *Ustulina* was different.

This being an unbranched germ tube it was reasonable to assume that it would show a growth increment equal to the total growth of the main axis plus the branches of the fungus used by Smith. It does not. If the logarithm of the length is plotted against time a line is obtained which is concave to the time axis in all the three examples. If, however, the logarithm of the length is plotted against the logarithm of the time (for the main period of growth only) the points then fall on a straight line. This state of affairs is illustrated in Fig. 4.

This type of growth can be represented by the equation

$$\log y = \log a + k \log t,$$

or, simply,

$$y = at^k.$$

The value of k varies with the germ tube. The average of twenty germ tubes gives a value of k which is approximately $= 1{\cdot}9$; the fast-growing hypha gives k approx. $= 2{\cdot}4$, while in the slow grower $k =$ approx. $1{\cdot}7$. This growth rate is not exponential and the difference between this result and that of Smith is most probably due to the influence of a constant "retardation factor" which is apparently present in this fungus, under the above conditions, and apparently absent in that used by Smith.

The assumption receives support from the work of White (1936) who found much the same state of affairs in the growth of *Lemna*, the retardation factor there being potassium deficiency. He refers to similar results by Gregory (1921, 1928) and expresses the opinion that this relationship may well be of general application to growth that would have followed the compound interest law but for the presence of a deleterious or deficiency factor.

The retardation factor was not determined for the germ tubes of *Ustulina*, but it may have been a constantly diminishing supply of oxygen.

IX. FACTORS INFLUENCING GERMINATION

Investigation of the factors influencing germination is complicated by the necessity of attempting to take them one by one in order to test their individual effect, whereas it is obvious that the factors conditioning any physiological process must be regarded as inter-dependent and wholly effective only when working in correlation.

In these germination experiments the following factors are regarded as the most important:

Internal:

The physiological condition of the spores.

Environmental:

Temperature.
Humidity.
Substrate.

(*a*) The physiological condition of the spores

This is the primary consideration in germination, and the external factors operate only within the limitations imposed by it. It is the most difficult factor to estimate and is not subject to control. It can, however, to some extent be allowed for.

It is convenient to postulate three phases in the physiological condition of the spores. These are here referred to as:

(1) The pre-mature phase.
(2) The mature phase.
(3) The post-mature phase.

(1) The pre-mature phase covers an unknown period of time during which the spores are ripening. Any attempt to germinate spores in this condition is unsuccessful. The phase cannot be ignored, however, as it is part of the developmental process leading to maturity, and these immature spores may be encountered in experimental work, particularly in material collected earlier than October.

(2) The mature phase begins when the spores are ripe and persists as long as they maintain a more or less constant germination capacity. The exact duration of this phase is unknown but it seems to last for a short time only. While it lasts the internal conditions are at an optimum and—all external conditions being favourable—germination is rapid and complete.

(3) The post-mature phase is represented by a change in the physiological condition associated with a gradual and uniform decrease in germination capacity. The spores become progressively less responsive to external stimuli, and the phase terminates in the death of the spores. This phase begins very soon after the spores mature.

There is considerable overlapping of the phases, so that experimental results are not in strict accordance with theoretical expectation. Undoubtedly many of the erratic results commented on by other writers and encountered in the present work could be attributed to insufficient attention to the condition of the spores used.

During August and early September, many of the exuded spores were in the pre-mature state. These spores were unsuitable for experimental purposes; in this work therefore, as far as possible, spores in the last two phases only were used. The beginning of October was taken as the date when the majority of the spores are mature, or, when the proportion of immature spores is almost negligible, and experimental work was started then and continued for five months. Fresh material was collected at monthly intervals. The use of fresh material is important as, in the natural environment, fructifications continue to produce spores, and so maintain the mature period of the spore mass beyond the mature period of individual spores.

As the above three physiological phases are correlated with time they can conveniently be expressed in terms of "age" of the spores. In this sense spore age is considered from two points of view:

(1) Age of spores, dating from the time of removal from the host.

(2) Age of spores, dating from the normal commencement of the spore season (i.e. the beginning of October) if left on the host.

The following experiments deal with the effect of spore age (in the above sense) on their germination capacity, under the above two headings.

(1) Fructifications were collected at the beginning of October and kept in glass dishes in the laboratory at an approximately constant temperature of 15° C. During the first few days, spores exuded vigorously, but after this initial exudation no more were produced. Spores from these exuded masses were germinated in tap-water extract of beech and incubated at 25° C. for 48 hr. The percentage germination was then calculated. Similar tests were made at intervals of fourteen days till two successive experiments produced no germination. This happened after about ten weeks. It was assumed that detachment from the host inhibited further spore production, and as the spores already mature apparently exuded all together, the age of the spores used could be considered as dating from the time of collection or exudation.

This experiment was repeated with spores collected at the beginning of November, December, January, February and March.

(2) Though the period over which production and maturation of spores may extend is unknown, it is assumed that fructifications left on the host continue to produce a succession of spores for some considerable time. The early part of October being taken as the beginning of the spore season, it is evident that spores collected at the beginning of November, December, etc., though perhaps recently produced, would, in this second sense, be older than those produced in October. The fall-off is indicated by the percentage germination obtained as the result of a germination test made immediately after each monthly collection.

To facilitate comparison all the germination tests were carried out simultaneously. Approximately 45,000 spores were counted in this experiment, and the results, under both headings, are given in Table III and expressed graphically in Fig. 5.

From these results it will be seen that the fall-off in germination capacity, under these two headings, can be estimated as follows:

(1) *Dating from time of removal from the host.* The fall-off in germination capacity of spores collected at the beginning of October can be represented by an approximately straight line. It falls from about 70 % at the time of collection to 0 % in the middle of December, giving an average drop of about 30 % per month. Spores collected

Table III. *Summary of results of experiment on falling off in germination capacity due to the age of the spores*

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
10 Oct.	72·32	—	—	—	—	—
24 Oct.	61·04	—	—	—	—	—
7 Nov.	40·02	60·38	—	—	—	—
21 Nov.	28·29	45·97	—	—	—	—
5 Dec.	9·93	31·10	51·42	—	—	—
19 Dec.	1·97	17·19	37·72	—	—	—
2 Jan.	0·00	5·00	24·02	38·30	—	—
16 Jan.	0·00	0·00	17·35	28·70	—	—
30 Jan.	—	0·00	8·09	19·93	28·81	—
13 Feb.	—	—	0·00	6·07	13·98	—
27 Feb.	—	—	0·00	0·00	3·03	10·72
13 Mar.	—	—	—	0·00	0·00	3·01
27 Mar.	—	—	—	—	0·00	0·00

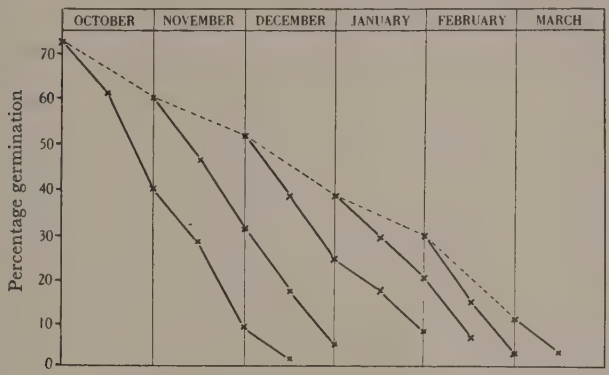

Fig. 5. Falling off in germinating capacity due to age of the spores.

at the beginning of November, December, etc., fall off at approximately the same rate. The later in the season the collection was made the more rapidly 0 % germination was reached, in that the initial percentage germination was not so high.

(2) *Dating from beginning of spore season if left on the host.* The fall-off is indicated by the dotted line joining the points which represent the percentage germination at the beginning of each monthly collection. Here again the fall-off is expressed by an approximately straight line, but the rate of fall-off is much slower than in spores removed from the host and kept in the laboratory. There is a drop from about 70 % in October to about 20 % in March, giving an average drop of about 10 % per month.

Where there is seasonal periodicity the importance of considering the age of the spores used in experimental work can hardly be over-

estimated. For instance, in an experiment performed at the beginning of December, when the spores used were from the October collection, their percentage germination (in beech extract) could be expected to be about 10, whereas freshly collected spores would give a percentage germination of about 50. The utility of Table I in this connexion is obvious, as it enables a correction factor to be applied to results which have been obtained at different times during the experimental period.

As a general result of the above experiments it can be said:

(*a*) That young mature spores may be expected to give maximum germination and that germination capacity decreases with increasing age of the spores.

(*b*) Spores from fructifications removed from the host fall off in germination capacity three times as rapidly as spores from fructifications which have been left on the host.

(*c*) The period of spore viability seems to be about six months, from October to March.

This question of spore germination in relation to age has been commented on by other workers. For instance, Child (1929, p. 341) found that spores one to four months old germinated well, but spores more than a year old germinated with difficulty or not at all. Ferguson (1902, p. 22) states that her results show that comparatively fresh spores are more satisfactory for cultural purposes than are older ones. The relation between spore age and germination capacity has an important bearing on the problem of parasitism. Brown (1934, p. 19), after stating that, in a general way, young spores germinate quickly but as they become older the percentage germination diminishes, goes on to point out that spores are capable of greater parasitic activity at their period of optimal germination than at other times. In *Ustulina* the optimal period is October and perhaps part of November.

(*b*) Environmental factors

(i) *Temperature*

An investigation into the temperature relations of the germination process demands consideration of three other factors:

(1) The physiological condition of the spores. The uncontrollable variation of this factor can be compensated for to some extent, by making due allowance for the age of the spores as already mentioned.

(2) The nature of the medium. This factor is completely controllable.

(3) The time factor. Control of this factor is possible by regulating the time of exposure.

The temperature relations will be dealt with under four headings:

(α) *Optimum temperature.*

This misused but convenient term will be employed here in the sense of Lehenbauer (1914), who described it as "That temperature at which there is the best growth during a given time period", with the substitution of "germination" for "growth".

Determination of optimum temperature. Determination of the optimum temperature for spore germination during a time period of 48 hr. was carried out in four different germination solutions. The experiment was done in two parts, the first in October when the spores were germinated in tap-water and in tap-water extract of beech, and the second in January using two nutrient media, starch medium and Czapek's medium. The hanging-drop method was employed and the drops were incubated at 10, 15, 20, 25, 30 and 35° C. respectively. The percentage germination was recorded and the germ tubes were measured. As, during this time period, no germination took place at 10 and 35° C., and little at 15° C., these are evidently not optima, and these results are not included in Table IV.

Table IV. *Determination of optimum temperature for germination*

	Age of spores: O 4/4				Age of spores: J 3/15			
	Tap-water		Tap-water extract		Starch medium		Czapek's medium	
Temp. ° C.	Av. % germ.	Av. tube length μ	Av. % germ.	Av. tube length μ	Av. % germ.	Av. tube length μ	Av. % germ.	Av. tube length μ
20	54·03	25·17	39·07	53·50	50·50	99·07	36·10	37·00
25	73·84	32·25	58·09	98·30	73·92	201·13	50·78	34·80
30	43·34	14·85	61·99	56·90	30·60	108·27	36·49	16·32

Judged on the basis of percentage germination, it seems that the optimum temperature varies to some extent with the germination medium, for, though in tap-water and the two nutrient media it is 25° C., in tap-water extract it appears to be 30° C., though germination at 25° C. is almost as good. There is consistent indication that 25° C. is the optimum temperature for the growth of germ tubes.

A consideration of all the four germination substrates gives the following averages for the total:

Temp. ° C.	Av. % germ.	Av. tube length μ
20	44·93	53·69
25	64·16	100·05
30	43·10	56·19

These results show conclusively that, in spite of the difference of the spore ages in the two sets of experiments and in spite of some slight variation in the medium, there is a very definite fixing of the optimum

at 25° C., both for percentage germination and growth of the germ tubes, and in both there is an almost equal fall in germination capacity on either side of the optimum to 20 and 30° C. respectively.

Within the conditions of the experiment, 25° C. is therefore indicated as the optimum temperature for spore germination, and this has been assumed in the subsequent experiments.

Effect of temperature on spores of different ages. In the above experiment it seemed that there was but little difference in percentage germination whatever the medium and whatever the age of the spores. As, however, the media used for the older spores were not the same as those used for the younger spores, and as it was therefore not possible to come to a definite conclusion as to the effect of age, the effect of temperature on spores of different ages was considered further.

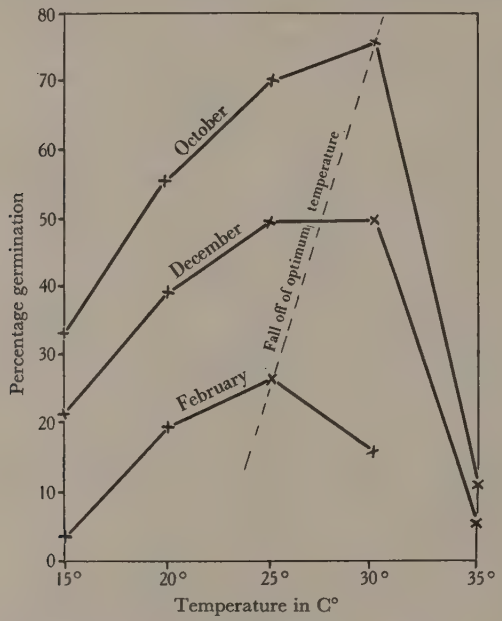

Fig. 6. Effect of temperature in relation to the age of the spores.

The spores were germinated in tap-water extract of beech for 48 hr. at each of the following temperatures: 15, 20, 25, 30 and 35° C. The spores were collected in October, December and February respectively. There was no germination at 35° C. in the February spores and no germination at 10° C. in any spores. The results are shown in Fig. 6 above.

It is evident from the above that, when using tap-water extract as a germination medium, the optimum temperature for October spores was in the region of 30° C. (This was confirmed on several occasions.) This optimum, however, gradually changes during the season to something between 30 and 25° C. in December and to 25° C. in February. This confirms the view that 25° C. can be regarded as optimum temperature.

Apart from this behaviour in tap-water extract the interesting feature of this graph is that it shows the gradual fall-off in the germination capacity consequent upon the increasing age of the spores. With any of the other germination media tried, the graphs of the October, December and February spores are respectively of the same type, and the optimum temperature remains constant.

Generally speaking, each temperature exercises the same relative stimulus to germination on spores of different ages, but the absolute effect of the stimulus varies inversely with the age of the spores.

The above graph shows a similarity to those of other workers, e.g. Fawcett (1921, p. 207, Fig. 1), Brooks & Cooley (1917), etc., for mycelial growth at different temperatures, and stresses the idea that the internal developmental processes of the germinating spore, expressed in terms of percentage germination, are of the same nature as those which, later, can be expressed in terms of measurable growth.

It was found that the average germination rate for successive time intervals varied with the temperature but was always greatest at the optimum. Fawcett, on the other hand, working on the mycelial growth of certain fungi parasitic on *Citrus*, found that there was a tendency for the apparent maximum temperatures for growth to shift to the left (in the graphs) with each successive observation period. Lindgren (1933), working with the growth of some wood-destroying fungi, stated that the growth rate varied to some extent with the time of exposure, but that there was no definite progressive decrease in daily increment at higher temperatures, nor progressive increase of daily increment at lower temperatures. In the present experiments on the temperature effects on *Ustulina* it was found that while the daily increments showed no tendency to shift, the monthly increments did show the tendency to drift to the left, as indicated by Fawcett.

(β) *The influence of maintained temperatures on germination.*

In the previous experiment the time period was 48 hr. The present one is intended to show the effect on germination of a longer time. Spores, in hanging drops of tap-water extract, were incubated at 15, 20, 25, 30 and 35° C. respectively. The percentage germination was calculated at the end of 12 and 24 hr. and at subsequent intervals of 24 up to 120 hr. The experiment was performed with October spores; the results are given in Table V and graphed in Fig. 7.

Table V. *Effect of maintained temperatures on germination*

Time in hr.	Age of spores: O 2/2 Av. % germination at the following temperatures				
	15° C.	20° C.	25° C.	30° C.	35° C.
12	3·34	7·67	10·87	19·98	0·00
24	18·96	43·17	63·21	68·39	4·00
48	33·53	53·36	72·00	78·48	12·89
72	47·97	59·30	74·06	82·01	18·45
96	49·47	62·96	75·98	83·01	23·50
120	51·48	65·94	76·63	83·48	28·50

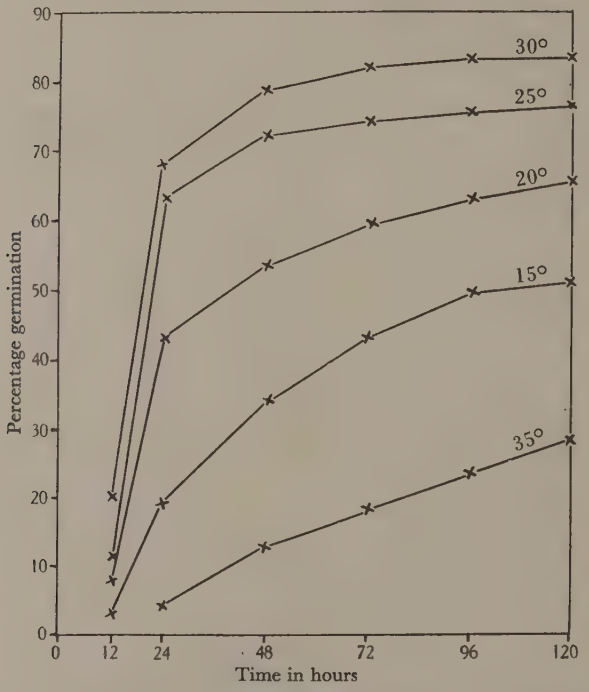

Fig. 7. Effect of different maintained temperatures in the germination of spores of the same age.

The characteristic feature of germination, as shown by the graph, is that at each of the temperatures near the optimum, i.e. 30 or 25° C., it is so rapid that almost 70 % germination is attained in 24 hr. At these temperatures the latent period varies from 6 to 12 hr., and is followed, during the next 12 hr., by a germination rate so vigorous that the graph is sent up almost vertically in relation to the time axis.

This is succeeded by a period of about 96 hr. in which there is little further germination. At temperatures removed from the optimum this initial burst of activity is progressively less marked so that at 15° C., on the suboptimal side, it is very slight, and at 35° C., on the supra-optimal side, it is non-existent.

The experiment indicates that when young spores are placed under optimum conditions of temperature and in a favourable germination medium, almost all the spores capable of germination do so within 48 hr. This justifies the use of the 48 hr. germination period adopted in most of the experiments.

The experiment was repeated at monthly intervals, but with the exceptions that the maximum percentage germination gradually fell off during the season and that the optimum temperature fell from 30 to 25° C. the results were so similar to those obtained with the October spores that they are not recorded.

The comparative response to maintained temperatures of 120 hr. by spores of different ages can well be illustrated by taking, from these results, the percentage germination obtained from spores collected in October, December and February respectively, at optimum temperature only. These are shown in Fig. 8.

Fig. 8 shows that the actual percentage germination reached in 120 hr. attained a maximum of 70–80 for October spores, 40–50 for December and 20–30 for February spores. It is evident that this maximum is almost reached after 48 hr., that continued exposure produces little further germination, and that the nearer the optimum temperature the greater the initial acceleration of the germination rate within the limit of the response of the spores. This limit is evidently determined by the age of the spores (dating from the beginning of the spore season), as each experiment was set up almost immediately after the monthly collection of the material.

In general, it is apparent that, at optimum temperature, whatever the age of the spores, a maintained temperature of 48 hr. is long enough to ensure the maximum germination possible. At the lower temperatures, e.g. at 15° C., a maintained temperature of about ten days would be necessary to reach the same degree of percentage germination. This fact is important as in these climates, the out-of-door temperature during the spore season is much nearer 15° than 25° C. This will be discussed later.

(γ) *Upper and lower temperature limits for germination.*

In certain previous experiments it has been shown that there is no germination at 10° C. on the lower, and at 40° C. on the upper side of the optimum temperature. As there was germination at 15° and at 35° C., and as no intermediate temperatures were available, the temperatures 10° and 40° C. have been taken as the lower and upper

temperature limits for spore germination. An attempt was then made to find the lower and upper thermal death-points of the spores.

The lower thermal death-point. Spores were germinated in tap-water extract. About forty hanging drops were incubated at each of the temperatures 0°, 5°, 10° and, as a control, 25° C. After incubation at these temperatures for 24 hr., five of the ring cells at each of the first three temperatures were transferred to optimum temperature (25° C.).

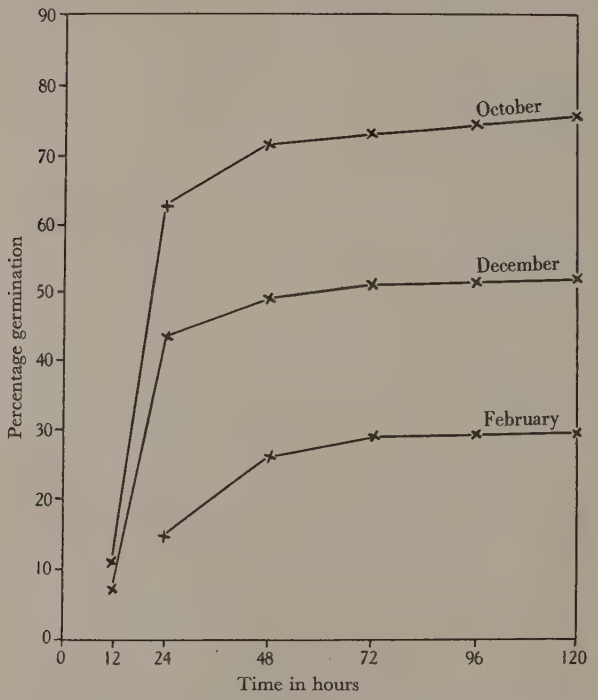

Fig. 8. Effect of a maintained temperature of 25° C in the germination of spores of three different ages.

They were left at optimum temperature for 48 hr. and the percentage germination of these and the control—which had remained at optimum temperature the whole time—was then calculated in the usual way. Similarly, five ring cells of each were transferred to optimum temperature at intervals of 24 hr., the last set to be transferred having been at the low temperature for 192 hr. The results obtained by counting approximately 40,000 spores are tabulated below and are expressed graphically in Fig. 9 (1).

Table VI. *Determination of the lower thermal death-point.*

Age of spores: O 3/3

No. of hours at low temp.	No. of hours at optimum temp.	Av. % germination at the following			Control	
		0° C.	5° C.	10° C.	No. of hours at 25° C.	Av. % germ.
24	48	65·63	47·86	44·43	72	59·30
48	48	80·62	60·33	49·16	96	62·96
72	48	63·57	66·53	53·89	120	65·94
96	48	53·60	70·36	57·08	144	65·98
120	48	32·53	67·16	58·56	168	70·02
144	48	28·53	62·19	63·95	192	72·99
168	48	22·28	55·75	64·80	206	71·47
192	48	21·98	51·46	68·03	240	75·00

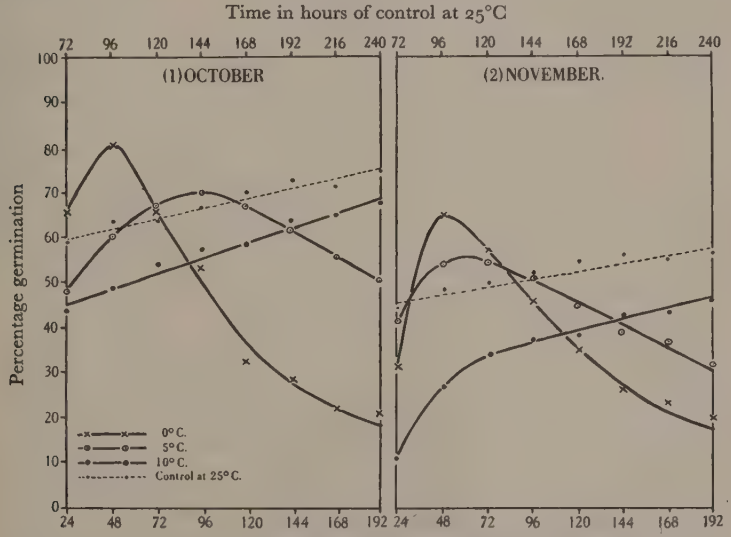
Time in hours of control at 25°C
72 96 120 144 168 192 216 240 72 96 120 144 168 192 216 240
(1) OCTOBER
(2) NOVEMBER.
Percentage germination
100 90 80 70 60 50 40 30 20 10 0
0° C.
5° C.
10° C.
Control at 25° C.
24 48 72 96 120 144 168 192 24 48 72 96 120 144 168 192
Time in hours, at low temperatures before transference to optimum

Fig. 9. Germination in relation to temperature. Determinations of lower temperature limits for germination.

Considering first the spores incubated at 0° C., it is evident from the graph that low temperatures do not kill the spores, but, on the contrary, stimulate the rate of germination. After 24 hr. at 0° C. and 48 hr. at optimum the germination percentage is 65, and this is higher than that of the control which has been at optimum temperature the whole time. After 48 hr. at 0° C. (and subsequent transference to optimum) the germination rises to 80 %, while the control after

the same period at optimum shows a germination of only 60 %. The high rate of germination must be due to the previous stimulation by the low temperature. Exposure prolonged beyond 48 hr., however, does not continue to stimulate germination; on the contrary, the germination percentage falls rapidly till, at 144 hr. it is only about 30, while the control has, in the meantime, steadily risen to about 70. This falling off after 48 hr. exposure cannot be due to delayed latency, for it has been shown that the latent period is shortened by such exposure. It must therefore be due to the intervention of some "depressant" factor in the sense of Barker (1933) or to the gradual death of the spores due to the low temperature. After 144 hr. further exposure causes a continued falling off, but this is more gradual, the percentage germination having dropped only to 20 at the end of the experimental period of 192 hr. Though circumstances prevented this experiment being carried further, there seems to be an indication that the germination rate continues to fall.

Subjection to 5° C. also stimulates but, as might be expected, this is less emphatic than at 0° C., the maximum germination not being reached till the spores have been exposed for 96 hr. The fall-off, following exposure prolonged beyond 96 hr., is much more gradual.

Incubation at 10° C. causes no stimulation to germination, but has the reverse effect. The 10° C. graph is not quite as high as it would have been had the spores been incubated at 25° C. without the previous incubation at 10° C. Moreover, the spores are not killed, but the percentage germination steadily increases, showing a normal temperature effect.

The general deductions from this experiment are that subjection to low temperatures—here 0° and 5° C.—for short periods stimulates germination which is apparent after subsequent incubation at optimum, but continued exposure causes the ultimate death of the spores. The lower the temperature the greater is the effect.

In order to verify these results this experiment was repeated with November spores and, in all essential features, the previous results were confirmed. For purposes of comparison these November results are shown along with the October results in Fig. 9 (2).

Increased germination as a consequence of exposure to low temperatures was found by Child (1929) who states (p. 429) that ascospores of two species of *Daldinia* were stimulated by being subjected to a temperature of $-5°$ C. for three months, but no such stimulation occurred in *D. concentrica*.

The above results are reminiscent of the "Vernalization Theory" of Maximov (1934), but as the present paper is concerned with the observed facts, no explanation will be attempted.

The upper thermal death-point. Spores were again germinated in tap-water extract. There had been slight germination at 35° C., so

the temperatures 40° and 45° C. were tested as possible thermal death-points. Spores were incubated at these two temperatures, but it was found that the periods of time used previously were of little use in this experiment. At 45° C. the period of exposure was progressively shortened but even after 1 hr. incubation there was no germination following the usual 48 hr. at the optimum. It can be assumed that spores are killed very quickly at 45° C., but as this temperature does not normally occur in nature during the spore season in these climates, no further work was done on this point.

Except for the variation in the time periods this experiment was carried out in exactly the same manner as the previous one. The only results included are the percentage germinations at 40° C. and at the control at 25° C. These are given in Table VII below.

Table VII. *Determination of upper thermal death-point*

Age of spores: O 3/3

No. of hours at 40° C.	No. of hours at optimum temp.	Av. % germ. at 40° C.	Control: No. of hours at 25° C.	Control: Av. % germ.
6	48	52·79	54	53·02
12	48	46·87	60	55·68
18	48	36·62	66	57·50
24	48	29·60	72	60·00
48	48	2·95	96	63·22

Table VII shows that exposure to a high temperature such as 40° C. does not lead to a higher rate of germination after transference to optimum. After 6 hr. at this temperature there is little difference between the percentage germination in the experimental material and the control. Prolongation of the exposure, however, causes a steady fall-off till after treatment for 48 hr. there is no germination at all.

Though exposure to the above temperatures caused no stimulation to germination in *Ustulina*, Child found that the allied species, *Daldinia vernicosa* was stimulated when subjected to high temperatures for short periods.

The work on temperature limits indicates that, from the standpoint of germination, the range of toleration is approximately from 15 to 35° C., and from the standpoint of thermal death-points the upper one is between 40° and 45° C., and the lower one is below 0° C., beyond which investigation was not possible with the apparatus available.

(δ) *Relation between temperature and probability of infection.*

It can be assumed that the more nearly the optimum temperature for spore germination coincides with the average out-door temperature during the spore season the greater the probability of infection. In

order to determine this relationship, the out-door temperatures from October to March were plotted together with the spore germination range as shown in Fig. 10.

The "stepped" graph shows the weekly average of daily readings of maximum and minimum temperatures taken in the shade at Oxford from October 1934 to March 1935. The "dot and line" graph shows single weekly readings of maximum and minimum temperatures taken at ground-level in a beechwood near Oxford.*

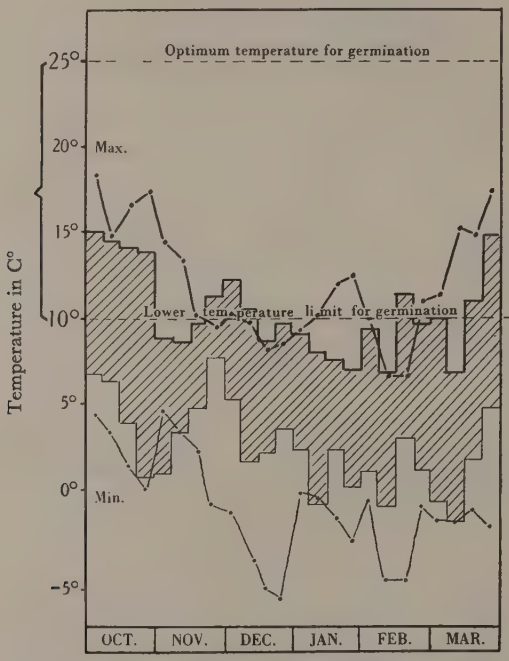

Fig. 10. Relation between maximum and minimum temperatures in nature and lower temperature limit for germination (explanation in text).

The ranges of temperature included between the maximum and minimum do not quite correspond, but the greater range in the beechwood temperatures includes the other range, and the average mean temperatures of the two are approximately the same. The mean temperatures have not been given, for as Fawcett (1925, p. 198) says: "It is probably seldom true that the physiological influence of a

* I am indebted to Mr G. M. Harris, B.A., B.Sc., a research student in this laboratory, for providing me with the beechwood temperature records.

changing temperature is quantitatively equivalent to the influence of a maintained temperature whose magnitude is that of the mean between the minimum and maximum temperatures." To give the mean temperatures, therefore, would be misleading, for, though they would be below the maximum and hence further from optimum temperature, the possibility of stimulation by an occasional drop to the minimum must not be overlooked.

Comparing the whole maximum-minimum range with the germination range it is obvious from the figure that these two do not coincide. If the mean temperature alone had been considered it would have come into the germination range only during the first two weeks of October and even then only very slightly. The maximum temperature is above the lower limit for germination only during October and the beginning of November and again during March, and only during October and March does the maximum temperature rise above 15° C. at which spore germination is relatively slow.

As a result of this comparison, with the exception of October (since March spores hardly germinate at all even at optimum temperature) it seems that during the spore season the temperature is a limiting factor which might conceivably inhibit spore germination, and hence infection by this means would be improbable or at any rate uncertain.

(ii) *Humidity*

The effect of relative humidity on spore germination was tested by drying off a film of spores in tap-water extract on a cover-slip which was then inverted and sealed over ring cells containing liquids of varying vapour pressure according to the method of Stevens (1916). Under these circumstances there was no germination even in a saturated atmosphere, and it was found that the spores will germinate only in liquid water or in solutions.

In nature a damp atmosphere seems to be essential for satisfactory exudation of the spores, and it is certain that spore emergence is more obvious and complete during and after a period of wet weather than during dry weather, when there appears to be no exudation of spores. In the laboratory, dry fructifications show no exudation and none will take place unless the fructifications are wetted or put into a damp atmosphere.

(iii) *The medium*

Nutrient aspect.

The experiments under this heading deal with the influence of the substrate on germination. The substrates used were the nutrient media in common use. With the exceptions indicated later they were made up, without agar, to the usual formulae from pure or "analytical" chemicals. The same chemical was sometimes obtained

from several sources for purposes of comparison, but there was no appreciable variation in the effect of the different samples.

Examination of the literature on this subject shows that there is no medium which is invariably favourable for spore germination. The varying influences of different media are most probably attributable to their respective nutritive values, and the object of the following experiments was not merely to determine those media which were favourable or unfavourable for germination, but to account for this variation in terms of the constituents of the media.

As a preliminary experiment, spores were germinated in the twelve media given below. The *p*H of the media was taken and, though the difference of the *p*H introduced a second variable, the media were not standardized as that would have necessitated the introduction of additional elements. The spores were incubated at 25° C. for 48 hr. The percentage germination and the germ-tube growth was then estimated, though only the former is included in the tables.

Table VIII. *Germination of spores in different nutrient media*

Age of spores: O 2/2

	Medium	*p*H	Av. % germ.
(1)	Malt	4·6	31·60
(2)	Oatmeal	5·8	67·64
(3)	Carrot	5·1	39·72
(4)	Potato	6·2	57·59
(5)	Potato dextrose	6·1	42·03
(6)	Potato sucrose	6·1	56·87
(7)	Starch	7·6	84·04
(8)	Richards's	4·9	86·89
(9)	Brown's	7·8	64·01
(10)	Czapek's	7·2	80·85
(11)	Kauffman's	5·8	72·53
(12)	Leonian's	4·5	88·90

Germination always occurred and, except on malt, carrot, and potato dextrose, it was above 50 %. Generally speaking, the natural media did not give such good results as the synthetic media. Whereas the average percentage germination on the six former was about 50 that on the six latter was about 80. Of the synthetic media, Brown's was the worst, and the best were Leonian's, starch and Czapek's media.

The natural media cannot be separated into their individual constituents, so the following experiments are concerned with synthetic media only. In general the media were made up according to the usual formulae, but as some were slightly modified, the actual composition is shown in Table IX.

The following two experiments are the same in purpose but differ in method. They are designed:

(1) To test the relative influence of each individual constituent on germination.

Table IX. *Composition of the synthetic media used in the experiments*

Medium	Starch	Richards's	Czapek's	Kauffman's	Brown's	Leonian's
Starch	10	—	—	—	—	—
Sucrose	—	50	30	—	—	—
Maltose	—	—	—	5	—	—
Dextrose	—	—	—	—	2	—
Laevulose	—	—	—	—	—	30
Asparagin	0·2	—	—	—	2	—
Potassium nitrate	—	10	—	—	—	2
Sodium nitrate	—	—	2	—	—	—
Calcium nitrate	—	—	—	0·5	—	—
Potassium chloride	—	—	0·5	—	—	—
Tri-potassium phosphate	1·25	—	—	—	1·25	—
Di-potassium acid phosphate	—	—	1	—	—	—
Mono-potassium acid phosphate	—	1	—	0·25	—	1
Magnesium sulphate	0·75	2·5	0·5	0·1	0·75	1

(2) To compare the germination in distilled water to which a constituent has been added with that in distilled water alone.

It can be assumed that if germination in water plus a constituent was greater (or less) than in water alone, the addition of the constituent was responsible for the increased (or decreased)germination.

In the first of these experiments, each constituent from a list of those comprising collectively the six synthetic media, was dissolved in distilled water in the proportion in which it is usually present in the medium. If any constituent was found in different proportions in several media, then an approximation was made. The results are shown in Table X.

Table X. *Effect of individual constituents on germination.* I

Age of spores : O 3/3

	*p*H	G. per litre	Av. %
Distilled water	7·0	0	56·66
+ Starch	6·8	10	71·59
+ Maltose	7·0	5	26·58
+ Sucrose	7·0	30	75·04
+ Dextrose	7·0	10	35·89
+ Laevulose	4·4	30	68·12
+ Asparagin	6·4	2	68·91
+ Potassium nitrate	7·0	10	61·30
+ Sodium nitrate	7·0	2	11·99
+ Calcium nitrate	7·0	1	96·38
+ Potassium chloride	7·0	1	41·16
+ Tri-potassium phosphate	9·4	1	61·06
+ Di-potassium acid phosphate	7·8	1	77·46
+ Mono-potassium acid phosphate	5·0	1	78·60
+ Magnesium sulphate	7·0	1	76·51

Table X shows that germination in the distilled water control was between 50 and 60%, and the only constituents associated with reduced germination were maltose, dextrose, sodium nitrate and potassium chloride. Increased germination in varying degrees occurred on all the rest. Calcium nitrate deserves special notice, as it produced almost maximum germination.

The second of these two experiments was designed to eliminate the chief objection to the first one, which was that the various constituents were in such unequal concentrations. In this experiment, therefore, the constituents were dissolved on a molecular basis which ensured that the concentrations were approximately the same. There is also an evaluation of certain elements. The results are shown in Table XI.

Table XI. *Effect of individual constituents on germination.* II

Age of spores: O 3/3

					G. per litre	*p*H	Av. %
Distilled water control						7·0	51·39
		C	H	O			
Maltose						6·9	42·89
	M/100	1·44	0·22	1·75	3·42		
Sucrose						6·9	62·85
Dextrose						6·8	22·63
	M/50	1·44	0·24	1·92	3·58		
Laevulose						4·8	67·34
KNO_3	*M*/50	K 0·78		NO_3 1·24	2·02	6·9	64·48
$NaNO_3$	*M*/50	Na 0·46		NO_3 1·24	1·70	6·9	11·84
$Ca(NO_3)_2$	*M*/100	Ca 0·40		NO_3 1·24	1·64	7·0	70·93
KCl	*M*/33·3	K 1·17		Cl 1·06	2·23	6·9	40·36
K_3PO_4	*M*/100	K_3 1·17		PO_4 0·95	2·12	9·6	51·37
K_2HPO_4	*M*/66·6	K_2 1·17		HPO_4 1·44	2·59	8·0	58·08
KH_2PO_4	*M*/33·3	K 1·17		H_2PO_4 2·87	4·04	4·8	74·10

The results shown in Table XI are interesting, as they confirm strikingly those of the previous experiment. In spite of some differences of concentration, the percentage germinations are very similar. The same four constituents are associated with reduced germination; the other germinations, though differing in degree, show the same relative response to the influence of the respective constituents. The only exception to this is provided by calcium nitrate which, in spite of increased concentration, gives a distinctly lower percentage. Starch and asparagin, which appeared in the first table, were omitted from the second; the former because it was no better than the individual sugars and was probably reduced to these, and the latter because, though generally used as a source of nitrogen, it might complicate matters by acting as a source of carbohydrate as well. These results will be discussed on the basis of the second table.

The carbohydrate supply. This was confined to four sugars. It appears that dextrose (though several different samples were tried) is not a

good source of carbohydrate. The only synthetic medium containing this sugar is Brown's, and that medium invariably gives relatively poor germination. Maltose is unsatisfactory, due probably to its breaking down to dextrose. The only medium in which this sugar is used is Kauffman's, which usually gives good germination, probably because of the calcium nitrate and in spite of the sugar. Sucrose and laevulose are both equally satisfactory but as the previous evidence indicates that it is only the laevulose part of the reduction products that is readily utilized, it appears that the ideal sugar for germination is laevulose. The only medium which has this as the sole source of carbohydrate is Leonian's, and this gives the best germination percentage of all the media tried. The media having sucrose as the only sugar, viz. Richards's and Czapek's, both give very good germination.

The source of nitrogen. It is apparent at once that sodium nitrate is not at all satisfactory, though, curiously enough, Czapek's medium, which gives good germination, contains this salt. The high percentage germination on this medium is probably due to the presence of sucrose. Potassium nitrate and calcium nitrate are both good, though of the two the calcium salt appears to be slightly more satisfactory. Richards's and Leonian's media contain the former and Kauffman's medium contains the latter; these three media give good germination. It seems from among those tried, that the nitrates of potassium and calcium are the best sources of nitrogen.

The salts of potassium. Potassium chloride is not good. This salt is found in Czapek's medium, but as this also contains di-potassium acid phosphate it can be assumed that the effect of the chloride is not important. The three phosphates give an interesting series of increasing germination varying with the increase of the acid radical, the potassium remaining constant all through. This occurred in both experiments but more particularly in the second, due, most probably, to the increasing degree of concentration in the second experiment. It seems that tri-potassium phosphate gives a germination little better than that obtained in distilled water alone and hence is not the best salt to use. It is found in starch medium and in Brown's medium; the former is good and the latter is not good. Di-potassium acid phosphate is rather better. It is not generally used in media but, as will be seen by Table IX, is here used in Czapek's medium. The best source of potassium certainly seems to be the acid salt, as this gives a very high percentage germination. It is, moreover, found in Richards's, Kauffman's and Leonian's media, all of which give satisfactory germinations.

Magnesium sulphate. This salt, which is usually regarded as essential for the growth of mycelium, is found in all the media. Used alone it gives a high percentage germination, but whether it is essential for germination will be discussed later.

It is concluded from the above two experiments that the best constituents to use for a germination medium are laevulose, calcium nitrate or potassium nitrate, mono-potassium acid phosphate and magnesium sulphate. It is interesting to note that the best germination medium, i.e. Leonian's, is made up of those four constituents and no others, and, with the single exception of the 96 % germination on calcium nitrate in the second experiment, this medium gives a higher germination percentage than any other medium or constituent used alone. Richards's medium, which was almost as good, only differed in that sucrose replaced laevulose. It appears, therefore, that the media vary in their effect on the germination capacity directly with the presence or absence of the desirable constituents as indicated above.

The fourth experiment of this series was intended to demonstrate if all the four most suitable constituents were equally essential or, if not, what combination of any three or two of them gave the best germination. The constituents were also repeated individually in controls. Each constituent was present in the solutions so made up in a concentration of $M/100$. Table XII indicates the method of the experiment and shows the results.

Table XII. *Influence on germination of various combinations of the four most favourable medium constituents*

Age of spores: O 4/4

Constituents				*p*H	Av. % germ.
Laevulose	$Ca(NO_3)_2$	KH_2PO_4	$MgSO_4$	4·9	94·15
Laevulose	$Ca(NO_3)_2$	KH_2PO_4	—	4·7	90·18
Laevulose	$Ca(NO_3)_2$	—	$MgSO_4$	4·8	72·37
Laevulose	—	KH_2PO_4	$MgSO_4$	4·7	73·61
—	$Ca(NO_3)_2$	KH_2PO_4	$MgSO_4$	5·2	63·59
Laevulose	$Ca(NO_3)_2$	—	—	5·0	74·55
Laevulose	—	KH_2PO_4	—	4·7	72·49
Laevulose	—	—	$MgSO_4$	5·0	81·72
—	$Ca(NO_3)_2$	KH_2PO_4	—	5·2	75·95
—	$Ca(NO_3)_2$	—	$MgSO_4$	6·4	77·47
—	—	KH_2PO_4	$MgSO_4$	4·8	79·56
Laevulose	—	—	—	4·6	78·52
—	$Ca(NO_3)_2$	—	—	7·0	80·45
—	—	KH_2PO_4	—	4·8	80·34
—	—	—	$MgSO_4$	7·0	69·91

Table XII shows that the complete medium does give the best germination, though the absence of the magnesium sulphate makes little difference and, allowing for normal fluctuation, the medium without magnesium sulphate can be said to be almost as good. The other combinations of any three or any two constituents or any constituent taken by itself are all equally good but rather less so than the first two mentioned. It is necessary to note that this experiment

was done with O 4/4 spores which would in beech extract be expected to give about 40–50 % germination (see Table I), and hence it can be concluded that with fresh October spores almost any of the arrangements in the above table would give almost maximum germination. Experiments (not included in this paper) with spores collected in October and January respectively and germinated in nutrient media show that the beneficial influence of optimum nutrient conditions in the substrate varies inversely with the age of the spores.

In all these experiments the growth of the germ-tubes was noted though not recorded. In general the most favourable media, as indicated by the highest percentage germination, were those which gave the most vigorous growth of germ-tubes.

Though only six media and fourteen constituents have been tested, and though the relative proportions and concentrations of these have been almost ignored, sufficient has been done to show that it is possible to devise a medium which will produce maximum germination when due allowance is made for other contributory factors.

It is suggested that further work on this point, though admittedly desirable, is outside the scope of the present paper. References to work of a similar nature by other investigators will be deferred till the germination of conidia is dealt with from the same point of view.

Effect of hydrion concentration.

The percentage germination in certain of the experiments, e.g. in different germination media, indicates that the *p*H of the solution—and hence the influence of the *p*H of the "infection drop" in nature—may be a factor of considerable importance. This section of the work deals with the nature of this influence by determining the optimum *p*H for germination and the range of *p*H toleration under various conditions.

Spores were germinated in rain-water, tap-water extract, starch medium and Czapek's medium respectively. The media were adjusted to approximately *p*H 2, 3, 4, etc., by the addition of *N*/20 hydrochloric acid and *N*/20 caustic soda respectively, and were tested by the "capillator" method. Each solution was made up to 100 ml., the acid and alkali being expressed as a percentage. This method is not quite as accurate as that of Karrer & Webb (1920), for the medium is diluted, but, within these limits, the dilution was found to have little effect. The spores were set up in drops of the adjusted media and incubated for 48 hr. at 25° C. The percentage germination was then calculated.

As it is well known that alkaline solutions tend to "slip back" towards neutrality, a preliminary experiment was done to find out the extent of this slipping back, for if this were considerable the initial *p*H does not represent the *p*H present during the germination period.

Samples of the solutions (without spores) were tested immediately after adjustment and every 24 hr. for a period of 72 hr., and Table XIII shows the result on Czapek's medium, which can be taken as representative.

Table XIII. *Testing stability of* pH *in Czapek's medium*

The original pH of first medium = 7·4. The original pH of second medium = 7·2

Approx. pH	No.	% acid or alkali	Initial pH	After 24 hr.	After 48 hr.	After 72 hr.
2	1	28·0	2·0	2·0	2·0	2·0
	2	28·0	2·1	2·1	2·1	2·1
3	1	12·0	3·0	3·0	3·0	3·0
	2	14·0	3·0	3·0	3·0	3·0
4	1	10·2	4·1	4·1	4·1	4·1
	2	11·2	4·0	4·2	4·2	4·2
5	1	9·7	5·1	5·2	5·2	5·3
	2	10·5	5·0	5·1	5·1	5·2
6	1	7·5	6·1	6·1	6·1	6·1
	2	7·5	6·1	6·2	6·2	6·2
7	1	2·5	7·0	7·0	6·8	6·8
	2	2·5	7·1	7·1	7·1	7·0
8	1	1·0	8·0	7·6	7·0	6·5
	2	1·5	8·2	8·1	8·0	7·8
9	1	2·0	9·0	8·6	8·2	7·0
	2	3·0	9·6+	9·4	9·1	8·5

Table XIII shows that only at pH 8 and 9 is there any lack of stability, and there the drop from the initial adjustment to the pH after 48 hr. appears to be uniform, as the pH at 24 hr. is more or less the mean of the other two. In the experiments, therefore, the spores were germinated during the first 48 hr. after adjustment, and the pH of the medium was taken to be the mean of the initial pH and the pH at the end of 48 hr. I am not in agreement with Webb (1921, p. 333), who emphasizes the fact that in his experiments the pH is to be regarded as the initial pH of the medium.

Experience made it possible to ensure that the average was always so near pH 2, 3, etc., that the points could be plotted at those values. No attempt was made to test the change of pH of the medium during the germination period, as any such change is considered to be incidental to germination.

The results of the experiment are shown in Table XIV and expressed graphically in Fig. 11.

The results show conclusively that, in general, the optimum pH for germination is in the region of pH 6. This is established, not only by the percentage germination, but also by the growth of the germ-tubes which was noted though not included in the tables.

As expressed in terms of percentage germination (all the graphs show a remarkable consistency and similarity of type) there is a constant adherence to the optimum irrespective of the germination medium, though it is more marked in some experiments than in

Table XIV. *Effect of* pH *on germination in media adjusted by hydrochloric acid and caustic soda*

Age of spores: O 2/2–3

Approx. pH	Starch medium Av. % germ.	Czapek's medium Av. % germ.	Beech extract Av. % germ.	Rain water Av. % germ.
3	48·23	60·28	69·13	38·77
4	63·06	64·09	73·60	59·16
5	68·34	75·37	79·33	72·75
6	89·72	90·46	85·56	85·74
7	76·44	73·86	79·80	58·17
8	66·86	49·66	61·36	51·55
9	64·63	48·99	59·33	48·58

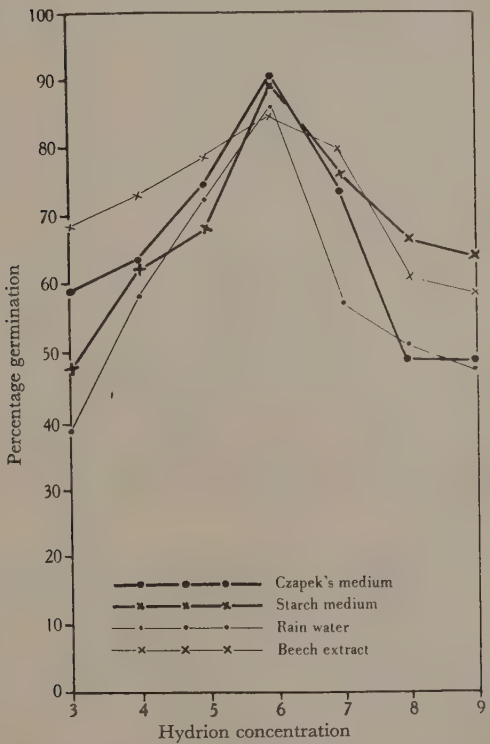

Fig. 11. Influence of pH on the germination of "October" spores in four different media adjusted by hydrochloric acid and caustic soda.

others. The range of *p*H toleration is comparatively wide, as (with the exception of rain-water) there is above 50 % germination over a range from *p*H 3 to 9. The limit of germination on the acid side was *p*H 2·5, at which there was no germination in any medium. A striking feature is the rapid rise from 0 % at *p*H 2·5 to from 40 to 70 % at *p*H 3. At the alkaline end it was not possible to determine the limit of germination, as there was no drop from *p*H 8 to 9, and beyond *p*H 9, owing to the limitations of the experimental method, no results were available. This toleration of alkalinity is not exceptional. Child, working with spores of *Daldinia vernicosa*, states that the extreme alkaline media of *p*H 9·6 stimulated the spores to almost maximum germination.

It is reasonable to assume that differences in the constitution of the germination medium might affect the *p*H, and in order to see if the actual method of adjustment made a serious difference to the results, the experiment was repeated with the same four media but adjusted with sulphuric acid and caustic potash. Allowing for minor differences, the results are similar to those of the previous experiment. The optimum remains constantly at *p*H 6, and the fall-off on either side is essentially the same as before. The similarity is emphasized if, instead of plotting the figures for each medium separately, the average of the first four graphs is plotted with the average of the second four, when it will be found that the two resulting graphs are practically superimposed.

It appears from this experiment that for all practical purposes it is a matter of indifference whether the media are adjusted with hydrochloric acid and caustic soda or sulphuric acid and caustic potash.

The effect of *p*H on spores which were older than those used in this experiment was tested next. The spores were collected in January, and from Table I it will be seen that the expected germination, in beech extract, would be about 40 % as against 70 % in October. The spores were germinated in the same four media as before, and the media were adjusted by means of hydrochloric acid and caustic soda. The results are shown in Table XV and have been expressed graphically in Fig. 12.

These graphs show that the age of the spores makes a difference. The optimum is still *p*H 6, but the percentage germination is not so high, that is, the older spores are physiologically incapable of responding so markedly to the stimulus of even optimum *p*H. The graphs exhibit a general similarity of type with those of October spores, but, though the fall-off on either side of the optimum is still more or less symmetrical, it seems that it is more marked at the extremes of acidity and alkalinity.

The essential difference between the influence of *p*H on October spores and that on January spores can be illustrated by taking the

Table XV. *Effect of pH on germination in media adjusted by hydrochloric acid and caustic soda*

Age of spores: J 3/15–16

Approx. *p*H	Starch medium Av. % germ.	Czapek's medium Av. % germ.	Beech extract Av. % germ.	Rain-water Av. % germ.
3	36·41	26·41	16·42	18·97
4	47·27	38·53	30·06	35·97
5	60·48	47·48	46·27	52·48
6	80·54	63·36	67·35	65·99
7	50·06	48·33	48·07	40·00
8	41·29	29·66	35·13	32·54
9	28·52	44·87	14·99	29·04

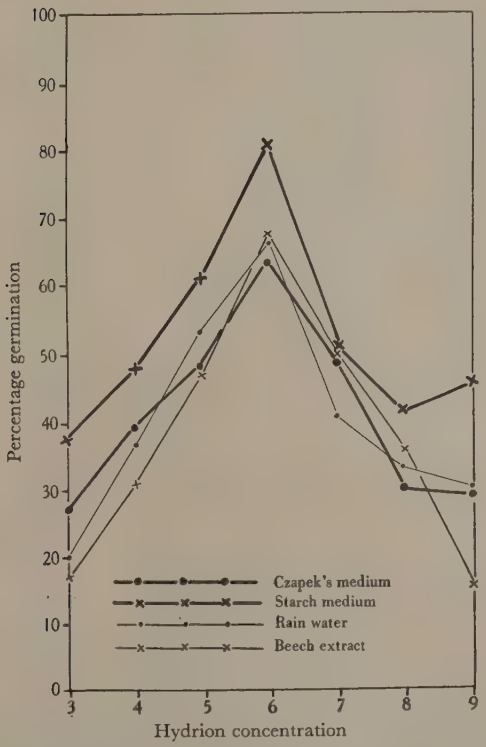

Fig. 12. Influence of *p*H on the germination of "January" spores in four different media, adjusted by hydrochloric acid and caustic soda.

average percentage germination in all the four media for October spores and comparing it with the average, again in all four media, for the January spores. The media are all adjusted with hydrochloric acid and caustic soda, so the only point of difference is the age of the spores. The results are expressed in Fig. 13 below.

This figure is a very adequate representation of the effect of *p*H on spores of different ages and well expresses the general impression obtained from considerable experimental experience.

As would be expected, the percentage germination is less in the older spores, but this fall-off is more marked at the extremes of the range of toleration than it is at the optimum. As stated before, the expected drop in germination (in beech extract) would be about 30 %. At the optimum *p*H, however, it is, on the average, only 20 %, and, in very favourable media, e.g. starch medium, the drop is only about 10 %. At the extremes of *p*H 3 and 9, however, the drop is, on the average, in the region of 30 %.

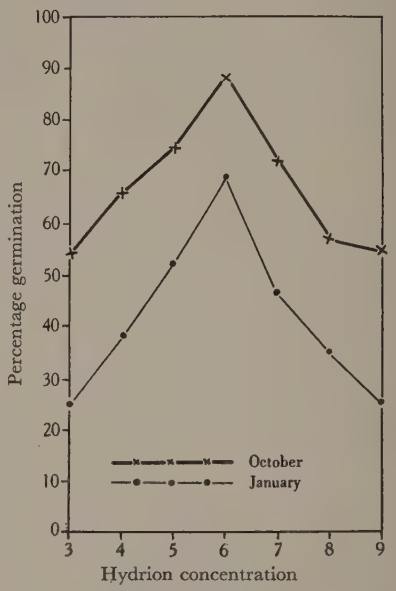

Fig. 13. Comparison of effect of *p*H on the average germination of "October" spores with that on "January" spores.

The fall-off in germinating capacity due to age is less if the spores are germinated at optimum *p*H, and increases progressively as the *p*H is removed from the optimum either towards acidity or alkalinity. Moreover, the tendency towards a rise in percentage germination from *p*H 8 to 9 is less obvious.

From the standpoint of percentage germination, it appears that spores of *Ustulina*, though remarkably tolerant over a wide range of *p*H, do, nevertheless, show a marked preference for that part of the range which is at or near the optimum, while toxicity of hydrogen and hydroxyl ions appears to be approximately equal.

The growth of the germ-tubes confirms this conclusion. The germ-tubes at the optimum *p*H were usually one from each spore, long, straight and unbranched. This state of affairs extended to about one degree on either side of the optimum, but, beyond this, the tubes were not so well grown. At the acid end the tubes were numerous, up to four from each spore, and invariably branched and twisted.

This agrees with the statement of Webb (1921, p. 316) that all fungi show abnormal germ-tubes in the most acid cultures allowing germination. At the alkaline end, tubes tended to be one or two from each spore, straight but very short, and this applied even where there was increased germination at the extreme of alkalinity. This point is also commented on by Webb. It does not always follow that good germ-tube growth corresponds with the optimum *p*H for germination, for Child (1929, p. 451), germinating the spores of *Daldinia concentrica* in Pfeffer's agar, found after 48 hr. that the optimum *p*H for germination was 5·6, but that the growth of the germ-tubes was most rapid at *p*H 7·6.

X. INFECTION

(*a*) Germination of spores in different timber extracts

As *Ustulina* is a parasite of various kinds of trees, the germination capacity of the spores in the respective water extracts of the different timbers was tested. Spores were germinated in tap-water extracts of seven different kinds of wood. In order to see whether spores germinated more readily in extracts of fresh wood than in those of seasoned wood, the extracts were made up from both green and seasoned wood. In each the percentage germination was calculated after incubation at 25° C. for 48 hr. It was found that almost always the length of the germ-tube was correlated with the percentage germination; therefore, though the germ-tube characteristics were noted at the time, they are not commented on here. The experiment was run in triplicate, and about 15,000 spores were counted. The *p*H of the solution was tested immediately before the experiment. The results are given in Table XVI.

Table XVI. *Germination of spores in different wood extracts*

	Age of spores: O 1/1			
	Seasoned		Green	
	*p*H	Av. % germ.	*p*H	Av. % germ.
Ash	6·9	8·0	7·2	33·53
Beech	6·8	73·14	7·1	66·94
Oak	4·6	2·21	5·4	13·42
Elm	7·2	30·30	7·1	26·41
Horse-chestnut	7·0	21·19	7·2	15·61
Lime	6·4	34·46	7·2	49·16
Poplar	7·2	41·25	7·2	25·55

Table XVI shows that germination in these different extracts is very variable. It is best in beech extract, whether green or seasoned wood is used, and worst in the oak extract, particularly with the seasoned wood. The seasoned ash extract also gives very poor germi-

nation. On the whole, no definite statement can be made as to the respective merits of green and seasoned wood as, in the different extracts sometimes one is better and sometimes another, and, if the total average percentage germination of the two sorts of wood be taken, the seasoned wood gives a total of 30·1 %, while the green wood gives a total of 36·2 %.

The facility with which spores of *Ustulina* will germinate in beech extract may indicate one of the reasons for the prevalence of *Ustulina* as a parasite on that tree, and, by the same argument, parasitism of lime, poplar and elm is a reasonable assumption. Decay of lime (Wilkins, 1936) and elm (Wilkins & Ellis, unpublished) has already been established, and *Ustulina* has been identified as having caused a timber decay of poplar.

The relation between germination in a given wood extract and ability to grow on the tree from which the extract was made has been described by Child (1929, p. 441). She obtained 54 % germination on *Platanus* decoction agar for *Daldinia concentrica*, which grows on *Platanus*, but there was no germination in this medium in two other species of *Daldinia* which are never found growing on *Platanus*.

(*b*) Penetration of wood

In order to test germ-tube penetration of wood, small blocks of beech—about $\frac{3}{8}$ in. cube—were cut so that they had faces which were exactly transverse, radial and tangential respectively. These were autoclaved in water and left standing in water in a Petri dish so that the wood was saturated and a damp atmosphere was ensured. Spores, taken directly from fresh fructifications, were placed on the blocks so that six of the blocks had spores on the transverse face, six on the radial and six on the tangential. The blocks were incubated at the four temperatures 15, 20, 25 and 30° C. for a week. At the end of that time they were sectioned, and the distance to which the hyphae had penetrated was measured. The average distance for each face of the wood at each temperature is given in Table XVII.

Table XVII. *Germ-tube penetration of beech wood*

Age of spores: O 1/1

Temp.	Transverse face	Radial face	Tangential face
° C.	mm.	mm.	mm.
15	1·5	0·2	0·5
20	2·5	1·0	1·5
25	5·0	1·5	2·5
30	2·0	0·25	0·4

All the blocks were penetrated. The penetration was best from spores on the transverse face, next best on the tangential face, and least on the radial face. As would be expected, hyphal penetration is

most rapid at the optimum temperature for germination and mycelial growth.

In order to see if penetration took place in other timbers, a similar experiment was set up in which spores were put on to blocks of ash, beech, elm, horse-chestnut, lime, oak and poplar respectively. These were incubated for a week at the same four temperatures as before, but the spores were put only on the transverse face of the wood. The degree of germ-tube penetration was measured in each and the average distances to which they had penetrated are shown in Table XVIII.

Table XVIII. *Germ-tube penetration of different kinds of timber*

	Age of spores: O 2/2 Average length of germ-tube in mm.			
	15° C.	20° C.	25° C.	30° C.
Ash	1·20	1·80	2·08	1·73
Beech	1·58	2·25	3·33	2·10
Elm	1·50	2·18	2·48	2·40
Horse-chestnut	1·20	1·58	1·88	0·83
Lime	1·65	2·33	3·00	2·03
Oak	0·0	0·0	0·0	0·0
Poplar	1·35	2·03	2·03	1·13

It is evident that penetration took place in all timbers except that of oak. On oak there was no penetration, and indeed, no germination of the spores on the surface of the timber. The blocks used were "seasoned", and as in the previous experiment of germination in timber extracts, the percentage germination in water extract of the seasoned oak was only about two; it would appear that seasoned oak, at any rate, is not susceptible to infection by *Ustulina* spores. Of the other timbers, the order of preference, from the standpoint of degree of penetration, is: beech, lime, elm, ash, poplar and horse-chestnut. This is rather a confirmation of the facts brought out in the experiment on germination in timber extracts as here also, beech, lime and elm head the list with poplar and ash very close up. In all, penetration is greatest at the optimum temperature of 25° C.

Under optimum conditions the rate of growth of germ-tubes in timber in a longitudinal direction is equal to or greater than the growth of the germinating hyphae when grown in a timber extract as shown in Table II. There it was shown that a fast-growing hypha will grow 340 μ in 24 hr., which is at the rate of 2·38 mm. in a week, while the average of twenty shows a growth rate of about 1·45 mm. per week. It is evident, therefore, that growth in timber, longitudinally, is more rapid on the whole than that in a comparatively favourable germination medium. Successful penetration does not necessarily imply subsequent parasitism, for, as Brown (1916) has remarked, fungi will often enter a host which they are quite unable

to parasitize and penetration is merely one of a number of steps which lead to parasitism. It is, however, one of the most important factors, for without penetration parasitism is impossible.

(*c*) Inoculation experiments

Twelve growing trees of lime and twelve growing trees of beech were used for this experiment. The trees were about five or six years old and well grown. At a point about 3 in., above ground-level, the surface was sterilized with alcohol and a hole was made with a borer. Spores, taken directly from a fresh fructification, were put into the hole by means of a needle, a drop of water was added and the hole was then plugged with a wood plug. Precautions were taken to prevent contamination. The inoculations were done in October and the trees left for twelve months.

At the end of twelve months, the trees were cut and examined. Positive infection had taken place in all. Round the inoculum there was a stained area which extended for about 1 cm., in a vertical and about $\frac{1}{4}$–$\frac{1}{2}$ cm. in a lateral direction. The stain was denser in lime than in beech. Sections were cut and examined for hyphae. These were found in the wood, mainly restricted to the stained areas, and extending to the limits, rarely slightly beyond, of the stain. Cultures of *Ustulina* were isolated from all the inoculated trees. Control experiments were considered unnecessary.

Although all the trees were infected, this result was not entirely satisfactory, as the progress of the mycelium in the timber was very slight, and the chances that the fungus would advance or, on the other hand, fail to advance are about equal.

XI. CONCLUSIONS

From the foregoing account it seems that the spores of *Ustulina* can germinate on, and penetrate, both dead and living timber, and will, under suitable conditions, produce infection. The extent to which this infection will result in the subsequent decay of the timber is not under discussion here. The inoculation experiments show that though there is no difficulty in producing infection, penetration is slow and the consequent mycelial growth is scanty. Inoculation into dead wood, on the other hand, results in rapid penetration, and it has been found (elsewhere) that decay invariably follows. It is suggested, therefore, that, in nature, infection takes place on dead timber, as, for instance, the surface of exposed wounds as indicated in the disease of lime previously described by me (Wilkins, 1936). Whether infection in general is produced by spores has not been determined, but, under favourable conditions, it is not impossible.

The favourable conditions referred to are two, viz. liquid water or

completely saturated wood, and a temperature which is above 10° C. for periods of not less than 24 hr. The former is not likely to be limiting, though it restricts the locality of infection. The latter, on the other hand, might well exercise an inhibitory effect. It has been shown (Fig. 11) that spores produced in temperate climates during the period October to March are under conditions which are sufficiently unfavourable to make infection by spores in general not impossible but at least improbable for a great part of the spore season.

The same argument would not be applicable to infection by spores in the tropics, and it is suggested that the relative infrequency of *Ustulina* disease in temperate regions is due to the absence of conditions which are favourable to infection by this means. I am in agreement with Van Overeem (1924), who, though asserting the pathogenic importance of *Ustulina* in Europe says, "Wenn sie in Europa als Parasit weniger auffällt, wird dies vielleicht durch das weniger günstige Klima verursacht", and I would suggest temperature as the most serious handicap.

Ustulina also possesses a conidial stage which is now being investigated along the same lines, and as conidia must also be regarded as a potential cause of infection it seems desirable to defer decision on this subject until evidence on the significance of the conidia in this connexion is available.

XII. SUMMARY

1. The paper attempts to determine the significance of the spore stage of *Ustulina vulgaris* in relation to the infection of standing timber in temperate climates.

2. The material was collected from fructifications on beech trees in various parts of the country during a period of six months in each of three successive seasons. The experimental method is described.

3. Shape and size of spores is commented on; the size of *Ustulina* spores, based on the average of some 500 measurements, is calculated as:

$$30{\cdot}82 \pm 0{\cdot}11 \times 7{\cdot}47 \pm 0{\cdot}03\,\mu.$$

4. Having determined a suitable germination medium, the initial stages in germination are described and the early growth rate of the germ-hypha measured over periods of 24 hr.

5. Of the factors influencing germination it is found that the physiological condition of the spores, expressed in terms of age, is the most important.

6. The optimum temperature for germination is 25–30° C., irrespective of age or environment. The germination range is approximately from 10 to 35° C. The lower thermal death-point is not determined but is certainly below 0° C., and the upper thermal

death-point is about 40° C. Relation between the range of outdoor temperature and the probability of infection is discussed.

7. Liquid water is essential for germination, and a saturated atmosphere is necessary for emergence of spores from the perithecia.

8. Investigation into the nutrient aspect of media suggests that the constituents of the media are of the utmost importance, and a medium approaching the ideal is described.

9. The optimum *p*H of the substrate is 6. The range of *p*H toleration is 3 to 9. The acid limit is about *p*H 2·5, and the limit on the alkaline side is not known but is beyond *p*H 9.

10. Germination tests in water extracts of seven different timbers indicated that, with the possible exception of extract of oak, these form good germination media.

11. Spores germinated on blocks of the same seven timbers penetrated all except oak. The degree of penetration is greatest at optimum temperature and most rapid in a longitudinal direction.

12. It is concluded that, in temperate climates, infection by spores is possible but improbable, and it is further indicated that the problem of infection cannot be decided without a thorough investigation of the conidial stage in this connexion.

My best thanks are due to my Research Assistant, Miss Margaret Ellis, M.A., B.Sc., for valuable help with this work and to my wife for checking the numerical results. I am very much indebted to the Department of Scientific and Industrial Research for a grant enabling me to employ a research assistant.

REFERENCES

Barker, J. (1933). "Analytic studies in plant respiration. IV. The relation of the respiration of potatoes to the concentration of sugars, and the accumulation of a depressant at low temperatures." *Proc. roy. Soc.* B, cxii, 316.

Brooks, C. & Cooley, J. S. (1917). "Temperature relations of apple-rot fungi." *J. agric. Res.* viii, 139.

Brown, W. (1916). "Studies in the physiology of parasitism. III. On the relation between the 'infection drop' and the underlying tissue." *Ann. Bot., Lond.*, xxx, 399.

—— (1934). "Presidential Address." *Trans. Brit. mycol. Soc.* xix, 11.

Child, M. (1929). "Preliminary studies in the genus *Daldinia*." *Ann. Mo. Bot. Gdn*, xvi, 411.

Fawcett, H. S. (1921). "The temperature relations of growth in certain parasitic fungi." *Univ. Calif. Publ. agric. Sci.* iv, 183.

—— (1925). "Maintained growth rates in fungus cultures of long duration." *Ann. appl. Biol.* xii, 191.

Ferguson, M. C. (1902). "Germination of the spores of *Agaricus campestris* and other Basidiomycetous fungi." *Bull. U.S. Bur. Pl. Ind.* xvi, 11.

Fisher, R. A. (1932). *Statistical Methods for Research Workers*, 4th ed. Edinburgh.

Gregory, F. G. (1921). "Studies in the energy relations of plants. I. The increase in area of leaves and leaf surface of *Cucumis sativus*." *Ann. Bot., Lond.*, xxxv, 93.

Gregory, F. G. (1928). "Studies in the energy relations of plants. II. The effect of temperature increase on area of leaf surface and dry weight." *Ann. Bot., Lond.*, xlii, 469.

Karrer, J. L. & Webb, R. W. (1920). "Titration curves of certain liquid culture media." *Ann. Mo. Bot. Gdn*, vii, 299.

Lehenbauer, P. A. (1914). "Growth of maize seedlings in relation to temperature." *Physiol. Res.* i, 247.

Lindgren, R. M. (1933). "Decay of wood and growth of some Hymenomycetes as affected by temperature." *Phytopathology*, xxiii, 73.

Maximov, N. A. (1934). "The theoretical significance of vernalization." *Bull. Herbage Publ. Series*, xvi.

Mounce, I. (1929). "Studies in forest pathology. II. The biology of *Fomes pinicola* (Sw.) Cke." *Bull. Dep. Agric. Can.* iii, N.S.

Petch, T. (1928). "The parasitism of tea root disease fungi." *Tea Quart.* i, 10. (*Rev. appl. Mycol.* 1928, vii, 543).

Saccardo, P. A. (1882). *Sylloge fungorum*, i, 350.

Smith, J. Henderson (1924). "On the early growth rate of the individual fungus hypha." *New Phytol.* xxiii, 65.

Steinmann, A. (1923). "Aanvullende mededeeling over het optreten van *Ustulina* bij *Hevea* in Java." *Arch. v. Rubbercult in Ned-Ind. jaarg.* vii, 448.

Stevens, N. E. (1916). "Humidity relations of fungi in culture." *Phytopathology*, vi, 428.

Tomkins, R. G. (1932). "Measuring germination." *Trans. Brit. mycol. Soc.* xvii, 147.

Tunstall, A. C. (1922). "Notes on fungus diseases during season 1922." *Quart. J. Sci. Dep. Indian Tea Ass.* iii, 115. (*Rev. appl. Mycol.* 1923, li, 343.)

Van Overeem, C. (1924). "Über *Ustulina vulgaris* Tul. und *U. zonata* (Lév.) Sacc." *Bull. Jard. bot. Buitenz.* vi, 256.

Webb, R. W. (1921). "Studies in the physiology of fungi. XV. Germination of the spores of certain fungi in relation to hydrogen ion concentration." *Ann. Mo. Bot. Gdn*, viii, 283.

White, H. L. (1936). "The interaction of factors in the growth of *Lemna*. VII. The effect of potassium in growth and multiplication." *Ann. Bot., Lond.*, l, 175.

Wilkins, W. H. (1936). "Studies in the genus *Ustulina* with special reference to parasitism. II. A disease of the common lime (*Tilia vulgaris* Heyne) caused by *Ustulina*." *Trans. Brit. mycol. Soc.* xx, 133.

SOME FUNGI ON THE YEW

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(With Plate IV and 3 Text-figures)

The fungi discussed in the following paper have all been obtained on the leaves of yew trees in the neighbourhood of Edinburgh, and the three following have proved to be the most interesting of those studied in pure culture.

Sphaerulina Taxi (Cooke) Massee

This fungus was first obtained from Cornwall and exhibited by the Rev. J. T. Boscawen to the Scientific Committee of the Royal Horticultural Society in 1878, when it was suggested that it was *Sphaeropsis Taxi* Berk. or some allied fungus. Cooke, to whom the specimen was sent for examination, regarded it as a new fungus to which he gave the provisional name of *Sphaerella Taxi* (1878*a*), which he later confirmed (1878*b*). He believed that it was a saprophyte, or at most a secondary parasite, but a year later (1879) he came to the conclusion that it was really the cause of the disease in the trees.

Smith (1884) published a popular account of this fungus with greater detail, and as a result Berkeley & Broome (1885) attributed the name *Sphaerella Taxi* to him when they recorded it as "...abundant, Sibbertoft (Northants), 1884". Smith published the first figure of this fungus in his account, and mentioned that the spores are multiseptate. He stated that the disease had spread during the previous six years, and was then found in Cornwall, Devon, Somerset and Dorset.

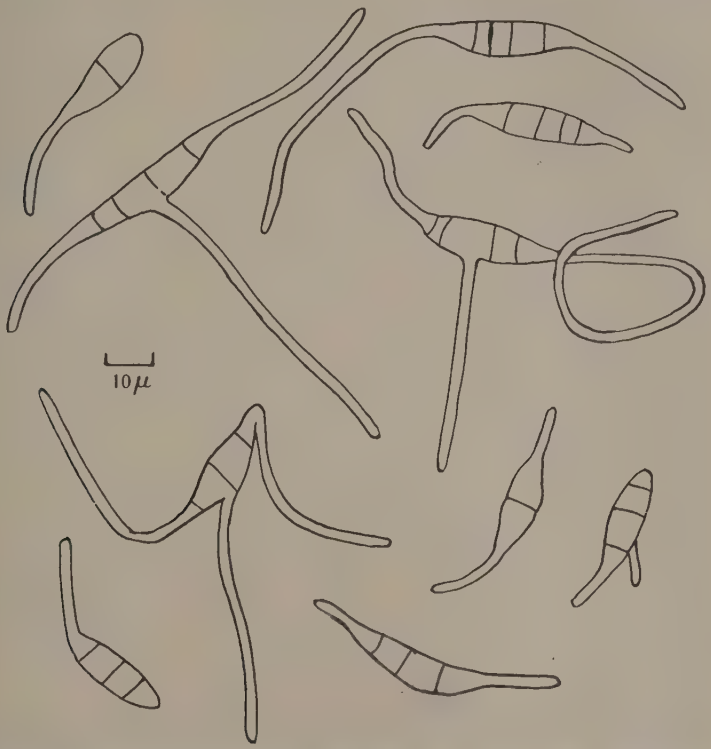
In a series of papers contributed to the *Journal of the Royal Horticultural Society* (1904), and later issued in book form (1906) Cooke gave a full description of the fungus *Sphaerella Taxi*.

In 1910 Massee transferred it to the genus *Sphaerulina* because of the multiseptate spores.

The next to deal with this fungus was Pilát, who (1926) published an account of *S. Taxi* (Cooke) Pilát on the yew in Czechoslovakia, and gave a partial history of the fungus known in Great Britain as *S. Taxi* (Cooke) Massee. He gave a full description of the species, pointing out that paraphyses were rare, but not absent, as stated by Massee, and that paraphysoids occurred occasionally. In every other respect his and Massee's descriptions agree, but (with an amended

description in Czech) he named the fungus *S. Taxi* (Cooke) Pilát n.comb.*

Pilát pointed out that this fungus was described by Oudemans (1900) as *Metasphaeria Taxi* Oud. from Nunspeet in Holland, and that Oudemans' description differed from that of Massee only in the statement that paraphyses are present. Pilát suggested that Oudemans



Text-fig. 1. Germinating ascospores of *Sphaerulina Taxi* (Cooke) Massee in sterile water.

had interpreted the paraphysoids as paraphyses, and was of the opinion that Cooke, Oudemans and Massee were all dealing with the same fungus.

There is considerable doubt regarding the exact nature of para-

* Under article 47 of the *International Rules of Botanical Nomenclature*, however, an alteration of the diagnostic characters of a group does not warrant the citation of an author other than the one who first published its name.

physoids, and as the difference between the latter and paraphyses has been used as a generic character, it is necessary to define these terms. Clements & Shear (1931) defined paraphyses as sterile hyphae between asci, and paraphysoids as plates of cellular tissue between asci, more or less resembling paraphyses. From a close study of a number of fungi, it is obvious that neither definition is satisfactory as it stood. The following definitions are therefore suggested:

Paraphysoids are cellular plates of tissue filling young perithecia before the asci develop amongst them. Paraphyses are sterile hyphae developing with and amongst the asci.

Oudemans placed *Metasphaeria Taxi* in the Pleosporaceae, and described it as possessing paraphyses, but made no mention of paraphysoids. Pilát claimed to have seen imperfect paraphyses (i.e. paraphysoids, according to him) in the perithecium, and stated that Oudemans seemed to consider imperfect paraphyses (i.e. paraphysoids) as homologous with paraphyses, which he himself could not accept, but compromised by stating: "... on ne trouve les paraphyses presque point, rares sont aussi les hyphes indistinct à la base (les paraphysoides)". From the Scottish material it was quite clear that paraphysoids as defined above, are absent from *Sphaerulina Taxi*, though present in *Physalospora gregaria* var. *foliorum*. Paraphyses (as defined) were absent from both species, and there was no sign of these imperfect paraphyses as described by Pilát. The walls of the empty asci might easily be mistaken for sterile hyphae.

Material obtained from a tree on the Forestry Commission Benmore Estate, Argyll, and stated to be *Metasphaeria Taxi* Oud., was found to be identical with *Sphaerulina Taxi* Massee, and showed no trace of paraphyses or paraphysoids.

Through the kindness of Prof. Westerdijk, and of Prof. Danser of Gröningen, some of Oudemans' original material from Nunspeet has been examined. Paraphyses and paraphysoids were entirely absent, so that the material agrees with *S. Taxi* Massee in every respect. The zoning of the perithecia on the leaf was not very marked on the material examined, but could nevertheless be detected.

Material of *S. Taxi* was obtained from Raith Park, Kirkcaldy, Fife (Pl. IV, fig. 1), at the end of March. After ten days in a damp chamber mature ascospores were produced, and the fungus was isolated in pure culture.

In sterile water the ascospores germinated within twenty-four hours, whether in the two-, three- or four-celled condition. As a general rule, two germ-tubes are produced at the same time, one at each end of the spore, but one of the germ-tubes may be produced from a central or subterminal cell instead. After germination, a two-celled spore lays down two additional cross walls, and rarely a triseptate spore will do so also, giving five in all. By that time the spore will have produced

a third germ-tube from the central cell, but no more than three are produced. Occasionally deformed spores may be found consisting of two cells and one germ tube only. There are no appressoria.

The material received in June from Benmore yielded ascospores of exactly the same size as those from Raith. They were triseptate already, but this is accounted for by the fact that the material was completely mature when received. Ascospore germination was identical, even five-septate spores being produced.

Ascospores were transferred to malt and yew agars. Growth on malt agar was slow—after fourteen days the mycelium was only one tenth of an inch in diameter, but on yew-extract agar it had a diameter of $1\frac{1}{2}$–2 in. If the mycelium produced no fructifications, growth was fairly rapid after the first week, whether on yew extract or malt agar, and in four weeks it had covered the medium in a Petri dish. When fructifications were produced the mycelium was small; it might be as little as three tenths of an inch in four weeks. Concentric brown rings were produced in the medium, which according to Klebahn (1918) are typical of the genus *Sphaerulina*.

In culture, plentiful conidia were produced, especially on malt agar, and to a lesser extent on yew-extract agar, particularly if pycnidia were produced later. They may be budded off from any part of the mycelium, and may in turn bud off further conidia. They are hyaline and measure $33–37 \times 5\,\mu$; at first unicellular and rod-like, they are later divided by septa. On malt agar a very large number of conidia are produced as a fluffy white mass on the medium, and, like the ascospores, may form mycelium, conidia, and pycnidia. All this too is typical of *Sphaerulina*.

On malt agar no fructifications were produced from mono-ascospore isolations in five weeks, but on yew-extract agar they could be seen as small dark patches in the centre of the greyish mycelium within fourteen days. This difference did not hold in subcultures, however, as fructifications were formed at almost the same rate on both media. When mature they were found to be pycnidia, which were identified as *Cytospora taxifolia* Cooke & Massee. This shows a close parallel with *Sphaerulina Rehmiana* (Klebahn 1918) and *Mycosphaerella Hippocastani* and *M. Ribis*, but Klebahn pointed out that the micro-pycnidial form of *Sphaerulina Rehmiana* occurred only in culture. It is not so with *S. Taxi*, however, as pycnidia and perithecia were obtained on the same leaves from Raith (Pl. IV, fig. 2), and also on material collected at Hopetoun, near Edinburgh, in November 1935.

This pycnidial form was first described by Cooke (1890) as *Cytispora taxifoliae* from Carlisle. It was next recorded by Oudemans (1898) from Nunspeet, Holland. Then Grove (1923) included it under *C. Pinastri* Fr. var. *Taxi* West. with the additional stations of Rugby and Glamis. Later (1935) he gave it as a synonym of *Cytospora Taxi*

Sacc. the pycnidial form of *Valsa Taxi* Fuckel, and mentioned that Cooke's specimen from Carlisle (*Cytospora taxifolia*) had spores 5–6 × 1 μ, whereas specimens from other stations had spores 7–9 × 1 μ (Worcs.) and 8–10 × 1·5 μ (Rugby). In 1927 Pilát and Macal published an account of *C. taxifolia* Cooke & Massee from Czechoslovakia, in which they expressed the opinion that *C. taxifolia* Cooke & Massee and *C. Taxi* Sacc. were two distinct species. They pointed out that this was only the second record of this fungus, the other being the type material from Carlisle.

Although Grove (1935) placed these two fungi together under *C. Taxi* it is quite clear that Pilát & Macal were justified in separating *C. taxifolia* and *C. Taxi*. Saccardo himself stated (1884) that the latter was the pycnidial form of *Valsa Taxi* Fuckel, whilst it has been shown above that *Cytospora taxifolia* is a pycnidial form of *Sphaerulina Taxi* Massee. There remains the difference in spore size to be explained; Cooke gave it as 3 × 1 μ, whilst Oudemans gave it as 4–5 × 1·5–2 μ, adding that Cooke's measurements were apparently not quite correct. Grove gave the measurements of Cooke's spores from Carlisle as 5–6 × 1 μ, and Pilát & Macal gave 3–4 × 0·7–1·2 μ for their Czechoslovakian specimen.

In order to settle the matter, Cooke's specimen from Kew was examined. On the sheet are three envelopes of a pattern often used by Cooke, and in his handwriting on each of them is his name, M. C. Cooke. On one is also written "*C. taxifoliae*" and on another "*Cytispora taxifoliae*, Dr Carlyle, Carlisle, 1890." In this latter packet the specimen is not *Taxus baccata*, but *Abies pectinata* (Pl. IV, fig. 4). In the other two the material is a mixture of *A. pectinata* and another form of *Abies*, but no *Taxus*. This sheet, the only one of Cooke's in the Kew Herbarium, has always been regarded as the type of *Cytospora taxifolia* Cooke & Massee, which Cooke (1890) described as occurring on the dead leaves of *Taxus baccata*. The spores of this specimen were measured and found to be 4·5–7 × 1·2–1·5 μ, which agrees fairly closely with that determined by Grove (1935) (5–6 × 1 μ) from Cooke's specimen, which must have been this *Abies*.

There is a *Cytospora* known on the leaves and twigs of *Abies pectinata*, namely *Cytospora Friesii* Sacc. (1884), the pycnidial form of *Valsa Friesii* Fuckel, and the description of this species agrees with Cooke's material on *Abies*. The spore size of *Cytospora Friesii* (Grove 1935), 4–5·5 × 1–1·5 μ (Rhodes 6–7 × 2 μ), is practically identical with that determined from Cooke's specimen, 4·5–7 × 1·2–1·5 μ. The specimen labelled *Cytispora taxifoliae* from Carlisle, and formerly regarded as the type of that species, is therefore *Cytospora Friesii* Sacc.

From Oudemans' description of the specimen collected at Nunspeet it would appear that he was not dealing with the fungus now known to be the pycnidial form of *Sphaerulina Taxi*. His spores were larger

and much broader (cf. above) and yellowish-orange instead of hyaline. He was very probably dealing with *Cytospora Taxi*, the pycnidial form of *Valsa Taxi* Fuckel.

In order to avoid additional synonymy it is best to assume that the species Cooke and Massee described was on *Taxus*, and to call it *Cytospora taxifolia* (Cooke & Massee) emend. Pilát & Macal.

In view of the deficiency of the descriptions of this species, a full account follows.

Sphaerulina Taxi (Cooke) Massee (1910)

Sphaerella Taxi Cooke (1878); *Metasphaeria Taxi* Oud. (1900); *Sphaerulina Taxi* (Cooke) Pilát (1926); *Cytispora taxifoliae* Cooke (1890); *Cytospora Pinastri* Fries var. *Taxi* Westd. p.p. (as quoted by Grove 1923); *Cytospora taxifolia* Pilát et Macal (1927).

Perithecia gregarious, epiphyllous, covering a part or the whole leaf surface, sunk in the host tissue and covered by the raised epidermis; subconical to oval, 140–186 × 125–165 μ (Pilát 120–180 μ), papilla short, 28–39 μ (Pilát 30–40 μ), not protruding above the epidermis. The wall consists of at least six outer layers of dark brown or black, laterally compressed, thick-walled cells, 7·5–15 × 5–9·5 μ, and 2–4 inner rows of hyaline, thin-walled cells, 12–17 × 7·5–13 μ. Asci in clumps, club-shaped, often curved, thin-walled, thickened at the apex, 8-spored, 57–75 × 10–13·5 μ (Pilát 45–65 × 10–15 μ). Paraphyses absent. Spores distichous, at first uniseptate, later 3-septate (in rare cases 5-septate after germination), often slightly constricted at the middle, 20–37·5 × 6·5–9 μ, average 28 × 7·5 μ (Pilát 15–20 × 5–6·5 μ).

The pycnidial form (*Cytospora taxifolia* (Cooke & Massee) emend. Pilát & Macal); Pycnidia solitary, scattered, completely immersed in the host tissue and occupying almost the whole thickness of the leaf, ostiole opening usually on the lower surface, but often on the upper surface; irregularly spherical to elliptical, 418–435 × 243–352 μ (Pilát & Macal 350–400 × 180–200 μ), black, plurilocular, with 3–5 incomplete septa. Wall 12–14 μ thick, consisting of 4–6 layers of small, thick-walled, oval cells, laterally compressed, 5–8·5 × 2·5–4 μ. Sporophores long, hyaline, simple or branched, 7–15 × 1·5–2 μ (Pilát & Macal 6–15 × 1 μ). Spores hyaline, rod-shaped, 3–5 × 0·9–1·2 μ (Pilát & Macal 3–4 × 0·7–1·2 μ).

Physalospora gregaria var. ***foliorum*** Sacc.

This fungus was first described by Saccardo (1878) from Padua, Italy. It was later found by Mouton (1886) at Beaufay in Belgium, and at the Château de la Motte near Bousval and a park in Ternath, both in Belgium, by Bommer & Rousseau (1890). In 1895 it was recorded from Nunspeet in Holland by Oudemans (1898) in company with *Pestalozzia funerea*.

It does not appear to have been reported again until Petrak & Sydow (1927), working on *Phyllostictina hysterella* (Sacc.) Petr., stated that they had been successful in proving by means of cultures that this species was the pycnidial form of *Physalospora gregaria* var. *foliorum*. This pycnidial form had been described by Saccardo (1881) as *Phoma hysterella* associated with *Physalospora gregaria* var. *foliorum* from a garden in Padua. It had also been reported by Bommer & Rousseau (1890) from Ternath in Belgium. In 1912 Diedicke described *Phoma allostoma* mixed with *P. hysterella* on the leaves of *Taxus baccata*. Van Luyk (1923) suggested that they were the micro- and macro-pycnidial forms of the same fungus. He pointed out that the spores of *Phoma hysterella* were very variable, and sometimes closely resembled those of *Gloeosporium taxicola* which he found on the same leaves. Grove (1935), quoting Saccardo, mentioned that *Phoma hysterella* was probably the imperfect form of *Physalospora gregaria* var. *foliorum*. Petrak & Sydow (1927) placed it in the genus *Phyllostictina*. Beyond the statement of relationship, they have published nothing, although Petrak (1934) has dealt extensively with the genus *Physalospora*.

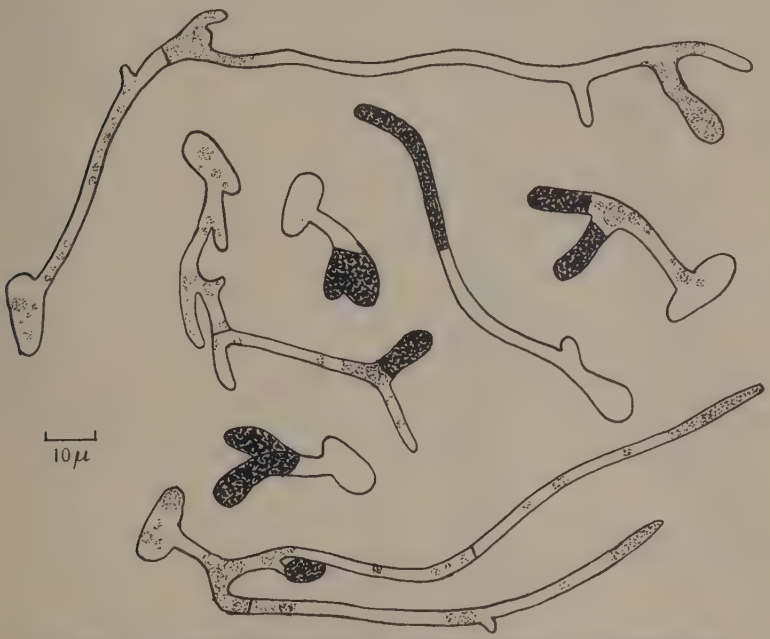
Material of *P. gregaria* var. *foliorum* was obtained from Old Glencorse Churchyard, near Edinburgh, in November 1934 (Pl. IV, fig. 7), and as the ascospores were mature, the fungus was isolated in pure culture.

In sterile water the ascospores germinated within eighteen hours, producing a single germ-tube from any part of the spore, but more usually from the sides than from the apices.

After forty-eight hours or longer in sterile water, appressoria were produced. If the spore had germinated rapidly, a branched germ-tube was produced, with practically no protoplasm left in the spore. After several days in sterile water, protoplasm collected in the tips of some of the branches, which became enlarged and the contents turned greenish brown. A cross-wall was laid down, cutting off that part of the branch from the rest of the germ-tube. If the spore had taken forty-eight hours or longer to germinate, only a short germ-tube was produced. This swelled up into an appressorium if left in sterile water. Large appressoria were divided by a cross-wall, but if small, several were formed on a single branched germ-tube.

Ascospores were transferred to malt agar, but failed to grow on

this medium. Oat, Dox and plain agars were all tried unsuccessfully, but yew-extract agar was found to be satisfactory. Growth was slow, but after fourteen days the mycelium had a diameter of half an inch. The whitish grey mycelium was very plentiful at first, but as it spread it assumed a steel-grey colour, and the aerial portion became more scanty, until only a thin membrane crept over the surface.



Text-fig. 2. Germinating ascospores of *Physalospora gregaria* var. *foliorum* Sacc. in sterile water.

On the fourteenth day the first signs of small black fructifications appeared in a ring on the surface of the medium. As the mycelium increased in diameter, concentric zones of fructifications were laid down, at first regularly, but later irregularly. A close examination showed that they were the pycnidia of the fungus *Phyllostictina hysterella* (Sacc.) Petr. (Pl. IV, fig. 8).

Monospore isolations of *P. hysterella* were made on malt and yew extract agar. On germination, a single germ-tube was produced, but very occasionally a second one could be observed. Appressoria were absent. The mycelium differed somewhat from that of the germinating ascospores, since it had a granular appearance and was always

brownish. Equally slow in growth, some produced pycnidia rapidly, others more slowly and after an interval of time, and then in the depths of the medium.

The young pycnidium was filled with parenchymatous hyaline cells, and later, a small, somewhat irregularly shaped cavity was formed, into which protruded more or less cylindrical sporophores. As the pycnidium developed, the spent sporophores became mucilaginous, while new ones arose from the cells beneath. This continued until all the parenchymatous cells had disappeared, and the cavity was filled with a mass of spores embedded in the mucilaginous remains of the sporophores.

Physalospora gregaria var. *foliorum* Sacc. (1878)

Phoma hysterella Sacc. (1881); *Phyllostictina hysterella* (Sacc.) Petr. (1927).

Perithecia subgregarious, solitary, occasionally in groups, generally epiphyllous, on the petiolar half of the leaf, and on the twigs. Perithecia globose, black, 183–234 × 138–202 μ, not quite covered by the epidermis, occupying half the thickness of the leaf, papilla if present very short, but usually absent; the wall consisting of 3–4 outer layers of thick-walled brown or black cells, 23·5 × 10 μ, and 2–3 layers of thin-walled, colourless cells, 16 × 7 μ. Asci club-shaped, thin-walled, 52–90 × 13–25 μ (Saccardo 85–90 × 15 μ), eight-spored. Spores distichous, ovate-oblong to egg-shaped, narrower at one end, ends rounded, 15–23 × 7–12 μ (Saccardo 20 × 7–8 μ), granular, hyaline, unicellular. Paraphyses absent.

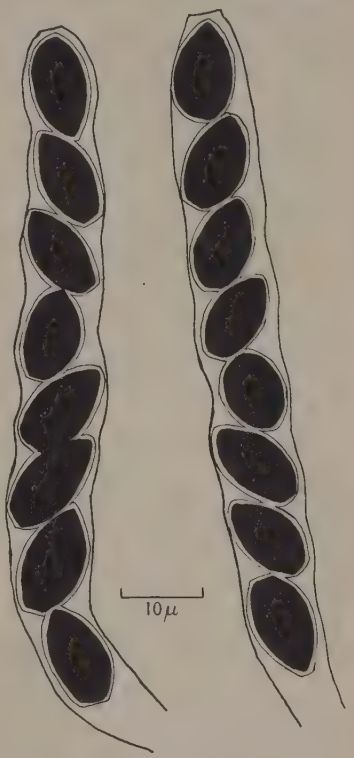
The pycnidial form (*Phyllostictina hysterella* (Sacc.) Petr.): Pycnidia subgregarious, on both sides of the leaf, more usually epiphyllous, often solitary amongst young perithecia of the perfect form; buried in host tissue, dark brown, spherical to ovoid, 185–208 × 140–179 μ (Petr. & Syd. 120–170 μ); ostiole small, often indistinct; the wall consisting of 3–4 layers of irregular, thin-walled, dark brown, elongated cells, 7·5–16 × 17–23·5 μ; parenchymatous cells filling young pycnidium 6·5–12 × 9·5–18·5 μ. Spores embedded in mucilage, broadly egg-shaped to elliptical, rounded at the ends, unicellular, hyaline, filled with coarsely granular protoplasm, 10–16 × 8–10 μ (Petr. & Syd. 10–15 × 7·5–8·5 μ). Sporophores straight, cylindrical, 6·5–11 × 2·5 μ (Petr. & Syd. 5–10 × 2–3 μ), often tapering at the point.

Anthostomella Taxi Grove

This species was described by Grove (1933) from material collected in Worcestershire. In November 1934 it was collected in Old Glencorse Churchyard on the same material as the previous species, and presented the following characters:

Perithecia sparse to subgregarious, singly or more rarely in groups,

on both surfaces of the leaf, but more commonly on the upper, completely sunk in the host tissue; spherical to ovoid, 207–342 × 195–250 μ, average 245 × 215 μ (Grove up to 200 μ in diameter), with a thin, dark brown outer wall consisting of 3–4 layers of brown, thin-walled, laterally compressed cells, 6·5–11 × 2·5–5 μ, and an inner wall of 2–3 layers of less compressed hyaline cells, 7·5–15 × 3·5–8 μ, papilla short, 46–56 μ, ostiole breaking through the somewhat raised epidermis; clypeus absent. Asci cylindrical, thin-walled, flattened at the tip, with a short pedicel, 80–92 × 11–13 μ (Grove 80–90 × 9–10 μ). Spores obliquely monostichous, ellipsoidal, pointed at one end, flattened at the other, dark brown, almost opaque, 11·5–14·5 × 8–10 μ (Grove 12–14 × 7–8 μ), with a thin, hyaline, indistinct, mucilaginous sheath, sometimes with a small tail of epiplasm. Paraphyses numerous, thread-like. Small rod-like structures, resembling conidia, can be found in the upper portions of the perithecial cavity; they are of unknown origin, but may be due to the disintegration of the paraphyses.



Text-fig. 3. Asci of *Anthostomella Taxi* Grove.

Grove's description and the above, although substantially in agreement, differ on a number of points such as the flattened tip of the ascus, the arrangement of the spores in the ascus and the shape of the spores, but the main point is the matter of the clypeus. Grove specifically stated that there was one present, and a clypeus is characteristic of the genus *Anthostomella*. A clypeus has never been observed on the Glencorse material, neither has there been any blackening of the epidermis (Pl. IV, fig. 5). This species would be more correctly placed in the genus *Leptomassaria* Petr. (1914) which apparently differs from *Anthostomella* only in the absence of a clypeus. Until a careful study of the generic characters of this group has been carried out, however, this species is best left in *Anthostomella*.

As the material was mature, it was placed in a damp chamber, and in eighteen hours spores were shot into hanging drops of sterile water.

They were lying in groups of six, seven or eight, each distinct from the other (Pl. IV, fig. 6). The odd one or two spores from each ascus were lying free inside the perithecium, as if they had hit the edge of the ostiole whilst the whole contents of the ascus was being shot out, and fallen back into the perithecium. Many of the spores have a small portion of the epiplasm attached to one end. As Grove stated, this is typical of several other species of *Anthostomella*.

The fungus generally appears to be associated with *Physalospora gregaria* var. *foliorum*, as the two occurred together on the Glencorse material and on material collected by Borthwick in 1900 at Balbirnie Park, Markinch, Fife. Grove suggested (1933) that *Phoma allostoma* Died. was the pycnidial form of *Anthostomella Taxi*, and if this is so, then there is also Diedicke's record (1912) of the two pycnidial forms growing together (see p. 100).

Other fungi identified on the material collected included two *Gloeosporium* species, *G. Taxi* Karst. & Har. from Raith Park, and *G. taxicola* Allesch. renamed *Cryptocline taxicola* by Petrak (1925). The latter species appeared to be plentiful when it did occur, and was obviously only a saprophyte, although no other fungi were associated with it.

Grove (1937), unaware of Petrak's renaming, remarked that *Gloeosporium taxicola* was not a typical *Gloeosporium*. Although Allescher suggested that it was the pycnidial stage of *Phacidium Taxi* Fr., Grove suggested that it was more likely to belong to *Anthostomella Taxi*. Grove (1933) had, however, already suggested that *Phoma allostoma* was the pycnidial stage of that fungus. To his statement of relationship Grove (1937) added that *Anthostomella Taxi* may be a *Sphaerulina*. This statement appears to be erroneous, as *Sphaerulina* possesses hyaline multiseptate spores, and *Anthostomella* brown non-septate ones.

Sphaerulina Taxi is widely distributed in Scotland, and is undoubtedly responsible for the diseased condition of many yew trees. It shows a preference for the golden varieties, and may cause much damage to the trees in the course of a year or two. The perithecia ripen in spring and the spores immediately infect the individual leaves of the new shoots, but it is not till early autumn, when the leaves turn brown, that there are any outward signs of infection. The leaves are soon completely killed, and during the winter pycnidia and perithecia are formed on the upper surface, while saprophytic fungi appear on the lower surface. Perithecia are very much more common than pycnidia, and they are always epiphyllous, covering either the whole or part of the leaf (Pl. IV, fig. 3). The mycelium does not appear to spread from the leaf into the shoot, although it spreads back into the petiole and that part of the surface of the twig immediately associated with the petiole. If several leaves close together are infected, the stem may

become "ringed" and the shoot will die, but will not become infected with *S. Taxi*. Infected leaves are retained on the shoot for at least six months after the perithecia have been produced in profusion unless the tree is exposed to winds.

The method of infection of *Physalospora gregaria* var. *foliorum* is not known with certainty, but after entering, the mycelium spreads through the stem and twigs. In general, perithecia and pycnidia are produced only on the lower half of the leaf (Pl. IV, fig. 7). If the lower part of a branch is killed by the fungus, the upper part will naturally die, but the mycelium does not spread to it. This fungus appears to be uncommon in Scotland.

Anthostomella Taxi is a saprophytic fungus which produces only a very few perithecia on any infected tree. It appears to be uncommon in Scotland, but the absence of records may be due to the very scanty production of perithecia.

The author wishes to thank Dr Albert Pilát for material and copies of his papers; the Director of the Royal Botanic Gardens, Kew, Professor Westerdijk and Professor Danser for material; and especially Dr Malcolm Wilson for originally suggesting this work, and for constant help and advice.

Summary

1. *Sphaerulina Taxi* (Cooke) Massee is described and shown to have as its pycnidial form *Cytospora taxifolia* (Cooke & Massee) emend. Pilát & Macal.

2. The type material of *Cytospora taxifolia* Cooke & Massee is on *Abies pectinata*, not *Taxus baccata* as described by Cooke, and it is identified as *Cytospora Friesii* Sacc.

3. *Physalospora gregaria* var. *foliorum* Sacc. is described with its pycnidial form *Phyllostictina hysterella* (Sacc.) Petr.

4. *Anthostomella Taxi* Grove is described and shown to be variable in some of its characters.

5. *Gloeosporium Taxi* Karst. & Har. and *Cryptocline taxicola* (Allesch.) Petr. are recorded.

REFERENCES

Berkeley, M. J. & Broome, C. E. (1885). "Notices of British fungi." *Ann. nat. Hist.*, (5), xv, No. 2050.

Bommer, E. & Rousseau, M. (1890). "Contributions à la flore mycologique de Belgique." *Bull. Soc. Bot. Belg.* xxix, 205.

Boscawen, J. T. (1878). *Gdnrs' Chron.* (2) ix, 247.

Clements, F. E. & Shear, C. L. (1931). *The Genera of Fungi.* New York.

Cooke, M. C. (1878*a*). "Yew disease." *Gdnrs' Chron.* (2) ix, 274.

—— (1878*b*). "New British fungi." *Grevillea*, vi, 121.

—— (1879). "Yew disease." *Gdnrs' Chron.* (2) xii, 800.

—— (1890). "New British fungi." *Grevillea*, xviii, 73.

—— (1904). "Pests of the ornamental shrubbery." *J. R. hort. Soc.* xxix, 1.

—— (1906). *Fungoid Pests of Cultivated Plants.* London.

Diedicke, H. (1912). In *Krypt-fl. Mark Brandenb.*, ser. vii, ix.
Grove, W. B. (1923). "The British species of *Cytospora*." *Kew Bull.* 1.
—— (1933). "New or noteworthy fungi." *J. Bot.* lxxi, 251.
—— (1935). *British Stem and Leaf Fungi*, 1. Cambridge.
—— (1937). *British Stem and Leaf Fungi*, 11. Cambridge.
Klebahn, H. (1918). *Haupt- und Nebenfruchtformen der Askomyzeten.* Leipzig.
Luyk, A. van (1923). "Über einige Sphaeropsideae und Melanconieae auf Nadelhölzern." *Ann. mycol.* xxi, 133.
Massee, G. (1910). *Diseases of Cultivated Plants.* London.
Mouton, V. (1886). "Ascomycètes observés aux environs de Liège." *Bull. Soc. Bot. Belg.* xxv, 137.
Oudemans, C. A. J. A. (1898). "Contributions à la flore mycologique des Pays-Bas. XVI." *Ned. kruidk. Arch.* 3 ser., 1, 430.
—— (1900). "Contributions à la flore mycologique des Pays-Bas. XVII." *Ned. kruidk. Arch.* 3 ser., 11, 170.
Petrak, F. (1914). "Beiträge zur Pilzflora von Mähren und Oesterr.-Schlesien." *Ann. mycol.* xii, 471.
—— (1925). "Mykologische Notizen. VIII." *Ann. mycol.* xxiii, 1.
—— (1934). "Mykologische Notizen. XII." *Ann. mycol.* xxxii, 317.
Petrak, F. & Sydow, H. (1927). *Die Gattungen der Pyrenomyzeten, Sphaeropsideen und Melanconieen. Repert. sp. nov. regni veget., Beih.*, xlii, 1. *Die phaeosporen Sphaeropsideen und die Gattung Macrophoma.*
Pilát, A. (1926). "Nová sypavka na tisech v Čechách—*Sphaerulina Taxi* (Cooke) Pilát." *Lesnická práce*, v.
Pilát, A. & Macal, J. (1927). "*Cytospora taxifolia* Cooke et Massee, nová sypavková nemoc na tisech v Čehách." *Lesnická práce*, vi.
Saccardo, P. A. (1878–81). *Mich.* 1, 11.
—— (1882–84). *Sylloge Fungorum*, 1, 11.
Smith, W. G. (1884). "Disease of yew—*Sphaerella Taxi* (Cooke)." *Gdnrs' Chron.* (2) xxi, 827.
International Rules of Botanical Nomenclature, revised by the Fifth International Botanical Congress, Cambridge, 1935.

EXPLANATION OF PLATE IV

Fig. 1. Transverse section leaf *Taxus baccata* with perithecium of *Sphaerulina Taxi* Sacc. × 360.
Fig. 2. Transverse section leaf with young pycnidium of *Cytospora taxifolia* Pilát & Macal, and perithecium of *Sphaerulina Taxi* Sacc. × 400.
Fig. 3*a*, *b*. Leaves of *Taxus baccata* showing zoning of perithecia of *Sphaerulina Taxi* Massee. × 2.
Fig. 4. Specimen of Cooke's *Cystospora taxifoliae* Cooke & Massee, actually *Abies pectinata* with *Cytospora Friesii* Fuckel. × 2.
Fig. 5. Transverse section leaf with perithecium of *Anthostomella Taxi* Grove. Note absence of clypeus and no blackening of epidermis. × 400.
Fig. 6. Sterile water hanging drop preparation showing ascospores of *Anthostomella Taxi* Grove. Note mucilaginous sheath. × 300.
Fig. 7. Twig of *Taxus baccata* showing perithecia of *Physalospora gregaria* var. *foliorum* Sacc. on leaves and twig. × 1.
Fig. 8. Transverse section pycnidium *Phyllostictina hysterella* Petr. in culture. Note ostiole, which is often absent or indistinct. × 360.

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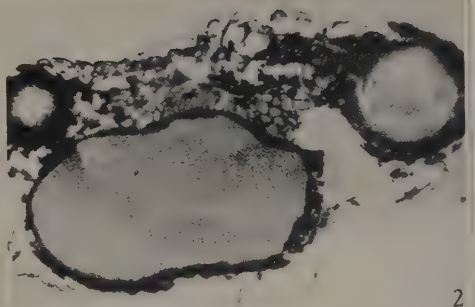
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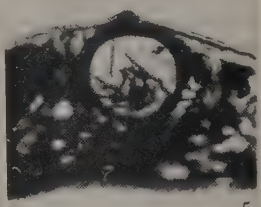
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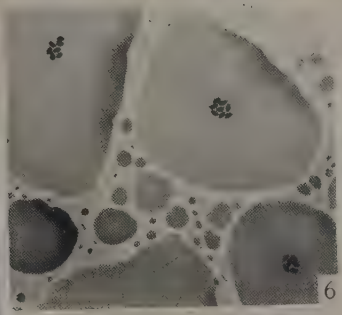
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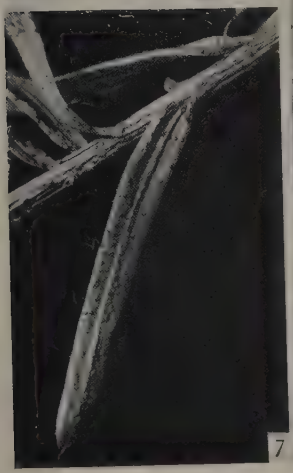
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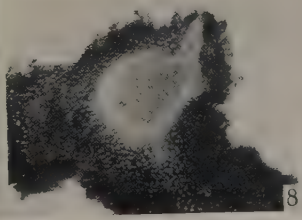
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3a 3b

TREMELLA TRANSLUCENS, A NEW SPECIES ON DEAD PINE NEEDLES

By H. D. GORDON, B.Sc.
Department of Mycology, University of Edinburgh

(With Plate V and 4 Text-figures)

The fungus forming the subject of this note occurs in comparative abundance along with a number of other fungi on dead leaves of *Pinus sylvestris* in a wood near Peebles, in southern Scotland. It is most readily recognized by soaking the needles in water, when the fructifications appear as hyaline, greyish white globules, 0·4–3 mm. in diameter, the majority measuring 1–2 mm. (Pl. V, fig. 1).

On drying, the fructification contracts to such a degree that it is recognized only by careful examination under a lens. It also assumes a dark colour, generally very dark brown or almost black. By reason of its inconspicuous appearance when dry it is probable that the fungus frequently escapes notice, and it may well prove to be comparatively widespread.

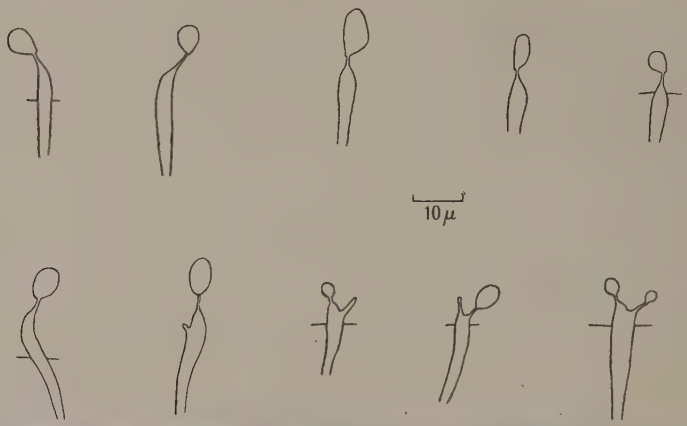
A transverse section of the leaf throughout the mesophyll, reveals abundant hyphae which become densely aggregated under the surface where the fructification breaks through. There is a short and relatively thick stalk-like portion, at first fairly distinct, but later becoming merged in the expanding fructification, which is then sessile and centrally attached. The leaf is blackened over a small area surrounding the insertion of each fructification.

The hyphae in the basal region of the fructification are closely arranged and more or less parallel, with comparatively little gelatinous matrix. As they diverge the amount of jelly increases until the hymenium is reached, where the basidia, in consequence of their greater diameter, form a dense layer. Outside this again is a layer of jelly through which the epibasidia eventually grow. The texture of the fructification is thus denser towards the centre, softer and more gelatinous farther out, but there is no suggestion of the firm, hard nucleus characteristic of the old genus *Naematelia* of Fries (Pl. V, fig. 2). The basidia are embedded near the surface of the jelly, and occupy the whole superficial area of the fructification; there is no differentiation into fertile and sterile surfaces.

The hyphae in the fructification have a diameter of 2·8–4·0 μ, while individual cells may be further enlarged, forming irregularly dispersed, vesicular swellings. Clamp connexions are frequent.

The basidia are spherical or slightly oval, usually measuring

10–14 μ in length and 9·5–13·5 μ in breadth. The length does not usually exceed the breadth by more than 1 μ; a similar excess of breadth over length is less frequent, but not rare. At times a marked increase in one or both dimensions may occur, one example measuring 23·9 × 14·6 μ. The basidia are of the usual tremellaceous type, and at a late stage of development the four cells frequently separate right to the base, a feature known in other members of this group of fungi. The separation was most noticeable in fructifications that had been kept very moist.

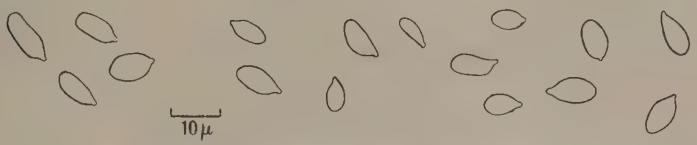


Text-fig. 1. *Tremella translucens*. Epibasidia with spores. The surface level of the jelly, where clearly defined, is indicated by a horizontal line.

When dry fructifications are brought into the laboratory and soaked in water they are generally found to bear an abundant crop of mature basidia, cruciately divided into four cells, but without epibasidia or spores. If such fructifications are then transferred to damp filter paper and kept under cover, further development takes place after a few hours. The epibasidia vary in diameter from 1·25 to 4·0 μ, so that the average is less than that of the normal hyphae, though the maximum is the same for both. A number of still thicker epibasidia were seen, bearing two sterigmata and spores (Text-fig. 1). The mature epibasidia vary so much in length that no average figure can usefully be given; measurements as short as 12 μ and as long as 100 μ have been obtained, the latter under very moist conditions. The epibasidium sometimes projects freely and to a variable distance above the surface of the jelly; at other times it just reaches this surface, immediately above which the spore is borne. The slender, tapering sterigma is usually 2–3 μ long, but its basal limit is not sharply defined from the epibasidium.

The basidiospores are oval, 7·1–11·8 × 3·7–6·2 μ, with an average about 9 × 5 μ. According to the direction of view both sides of the spore may appear convex, or one may be almost straight, but scarcely ever does one side present a concave appearance, which would result in the curved spore shape characteristic of *Exidia* and certain other genera of the Tremellaceae. The spore bears a small oblique apiculus at its base, immediately adjacent to the point of attachment to the sterigma (Text-figs. 1, 2).

The spores germinate readily in the presence of moisture. Three types of germination may be distinguished, though they intergrade somewhat; all three types were recorded for *Tremella* spp. by Brefeld (1888).



Text-fig. 2. *Tremella translucens*. Basidiospores.

Text-fig. 3. *Tremella translucens*. Basidiospores germinating in water; early stage.

(i) By repetition; the germ-tube rather resembles the sterigma, and bears a secondary spore more or less similar to the original basidiospore in size and shape. This is generally regarded as the normal mode of germination in *Tremella* (Pl. V, fig. 3 *a*).

(ii) By budding; a number of small yeast-like conidia or sporidiola are produced directly from the basidiospore (Pl. V, fig. 3 *b*).

(iii) The germ-tube grows out as a simple hypha or branched mycelium from which, sooner or later, yeast-like conidia are irregularly abstricted (Pl. V, fig. 3 *c*, and Text-fig. 4).

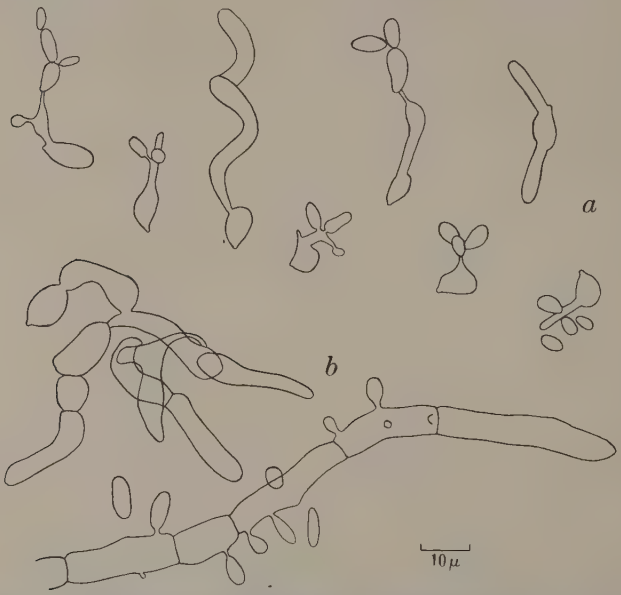
In (i) and (iii) the germ-tube may arise from any part of the spore, laterally, subterminally or terminally from either end (Text-fig. 3).

The first method, by repetition, was found to be the most frequent among spores germinating on the moist surface of the fructification,

and is probably the commonest in nature. The second method, by budding, was also fairly frequent in this situation.

Germination in hanging drops of water generally followed the second method, large numbers of yeast-like conidia being formed; the first and third methods also occurred, but less frequently (Pl. V, fig. 3).

Germination in a nutrient solution, such as dilute malt extract, resulted in greater luxuriance of growth, and germination by repeti-



Text-fig. 4. *Tremella translucens*. Basidiospores germinating in dilute malt extract solution. (*a*) After 24 hr., (*b*) after 45 hr.

tion was not observed (Text-fig. 4). Many spores followed the second method, while many others produced one or more germ-tubes; these sometimes formed a freely budding sprout-mycelium immediately, but they might attain a considerable length and complexity of branching before bearing conidia. The ultimate result was a luxuriant sprout-mycelium, from which yeast-like conidia were irregularly abstricted.

This fungus does not seem to conform to any published description. Perhaps the nearest resemblance is offered by *Tremella glacialis* Bourd. & Galz., in spite of the different type of substratum on which that species has been recorded, and a difference in habit which might be

connected therewith. The present species is somewhat larger, both in macroscopic and microscopic dimensions, particularly in the length of the spores, which are more elongated oval than those of *T. glacialis*. Neuhoff (1931) regards *T. glacialis* and the very similar or identical *T. Grilletii* Boud. as species of *Exidia*, on account of their spore shape. Whelden (1934, 1935) disagrees with this, and figures spores of *T. Grilletii* which certainly suggest that it should be retained in the genus *Tremella*. However that may be, the present species would appear to be correctly referred to *Tremella*: the hymenium covers the entire exposed surface of the fructification, leaving no sterile surface, and is perfectly smooth, without the ridges or papillae common in *Exidia*. The thick-walled, superficial hyphae recorded by Whelden in dry fructifications of *Exidia*, but not of *Tremella*, have not been observed in this material. The spores are oval, not curved, and germinate like those of *Tremella*; the septation of the spore, and the curved sporidiola characteristic of *Exidia*, do not occur.

Within the genus *Tremella*, this species finds its place in the section Tuberculiformes (*Nanotremella*) which have small smooth fructifications without lobes or furrows. Only three such species are listed as European by Neuhoff (1931), two of which are distinguished by their colour, as well as other characters. The third, *T. fusispora* Bourd. & Galz., is hyaline to milk-white, but is smaller than the present species, and is distinguished particularly by its spores, which are long and fusiform. *T. translucens* is therefore to be regarded as an additional member of this group.

Tremella translucens n.sp.

Erumpent, 0·4–3 mm. when moist, hyaline, greyish white, spherical or slightly flattened, of soft gelatinous consistency; when dry minute, hard, dark brown or black, with a central depression; basidia spherical or slightly oval, 10–14 × 9·5–13·5 μ; spores hyaline, oval, with an oblique basal apiculus, 7·1–11·8 × 3·7–6·2 μ, average 9 × 5 μ.

On dead leaves of *Pinus sylvestris*. Peebles, in southern Scotland.

Tremella translucens n.sp.

Erumpens, uda hyalina, albo cinerea, gelatinosa, subglobosa, 0·4–3 mm. lata; sicca minuta, dura, fusca vel atra, centro depressa; basidiis globosis vel late ellipsoideis, 10–14 × 9·5–13·5 μ; sporis hyalinis, ellipsoideis, basi oblique apiculatis, 7·1–11·8 × 3·7–6·2 μ, plerumque 9 × 5 μ.

Hab. in foliis emortuis *Pini sylvestris*, Peebles Scotiae australis.

The type material is deposited in the herbarium at the Royal

Botanic Garden, Edinburgh, and material has also been sent to the herbaria of the British Museum (Natural History) and the Royal Botanic Gardens, Kew.

The fungus described in this note was first observed by Dr Malcolm Wilson, to whom I am indebted for making material available, and for his help and criticism in the preparation of this description.

REFERENCES

Brefeld, O. (1888). *Untersuchungen aus dem Gesamtgebiete der Mykologie*, VII, 106–29. Leipzig.

Neuhoff, W. (1931). "Kritische Gallertpilze. II. Die europäischen Arten der Gattung *Tremella*." *Z. Pilz.* XV, 70–75.

Whelden, R. M. (1934). "Cytological studies in the Tremellaceae. I. *Tremella*." *Mycologia*, XXVI, 415–35.

—— (1935). "Cytological studies in the Tremellaceae. II. *Exidia*." *Mycologia*, XXVII, 41–57.

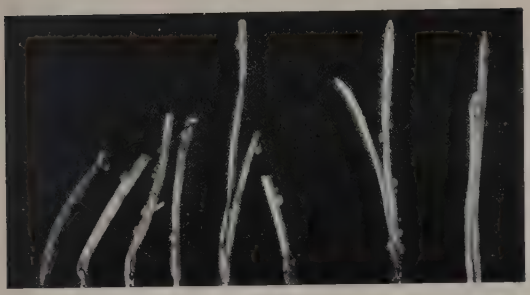
EXPLANATION OF PLATE V

Tremella translucens n.sp.

Fig. 1. Fructifications on leaves of *Pinus sylvestris*, slightly magnified.

Fig. 2. Thick hand section through a leaf of *Pinus sylvestris* bearing a fructification, to show the general structure of the latter, × 50. At either side of the fructification some of the small, spherical basidia have been displaced by pressure.

Fig. 3. Basidiospores germinating in water, (*a*) by repetition, (*b*) by budding, (*c*) by a simple hypha.



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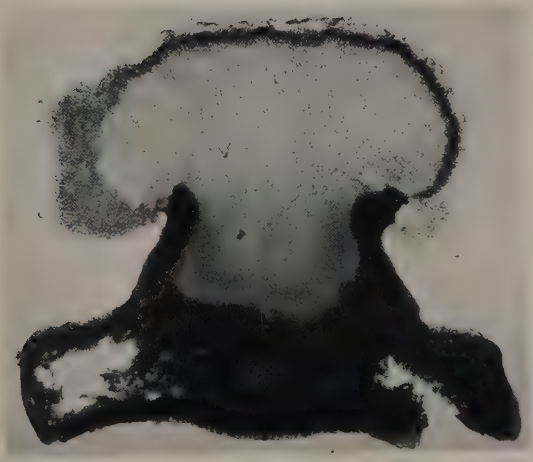

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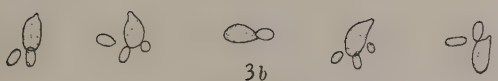

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NOTES ON *FUSARIUM AVENACEUM* ATTACKING THE LEAVES OF TULIPS IN GLASSHOUSES

By A. BEAUMONT and W. BUDDIN

Early in February 1931 and again in 1932 small lesions, up to 1 cm. across, were observed on tulip leaves, variety William Copland, in a greenhouse near Exeter. The lesions might easily have been mistaken for tulip fire, but on incubation in a moist dish a very different type of mycelium was formed. In a few dishes yellow spore masses appeared and the lesions enlarged rapidly. The spores of the fungus were 3-septate, curved and mostly 45–60 × 2–3 μ. Pure cultures were easily obtained and were sent to Dr H. W. Wollenweber, who identified them as *Fusarium herbarum* (Cda.) Fr. var. *tuberculariodes* (Cda.) Wr. In their book published in 1935, Wollenweber & Reinking (1935) included this fungus in the species *Fusarium avenaceum* (Fr.) Sacc.

In February 1931 E. R. Wallace reported *Fusarium* on tulip leaves in Lincolnshire. The cultures he had obtained were examined and it was confirmed that they were the same fungus as that from Exeter. The disease is apparently of frequent occurrence in Lincolnshire although never doing serious damage: Mr Wallace has observed it as early as 4 January. In more recent seasons it has been observed in Berkshire, Hampshire, Middlesex and Oxfordshire. It has been found only in forcing houses, with one exception, at Penzance, Cornwall in March 1932, when it was found out of doors on a few plants and was probably associated with mechanical injury.

The disease is probably not a new one. Oudemans (1919) recorded *Fusarium roseum* Lk. on the scapes of *Tulipa Gesneriana*, giving the reference to W. J. Hooker's *English Flora* v, Part II, p. 355 (1836), where *F. roseum* is stated to occur "on the stems of various plants, as beans, tulips, etc. Apethorpe, Norths. Rev. M. J. Berkeley."

It is probable that this was the same as the present fungus, which is closely related to *F. graminum* Cda. (syn. *F. roseum* Lk.), both belonging to the section Roseum in Wollenweber's classification.

Wollenweber & Reinking (1935), presumably describing conditions in Germany, state that *F. avenaceum* sometimes causes spots on leaves and stems of tulips "weakened by incorrect forcing". An unidentified species of *Fusarium* is associated with the rotting of the young shoots in Germany increasing after the boxes have been brought into the greenhouse for forcing (Höstermann, 1926; Ministry of Agriculture, 1928–32; Pape, 1936), and a similar occurrence was observed in England in 1932 (Ministry of Agriculture, 1932).

Field observations have shown that the disease is favoured by both high temperatures (70° F. or over) and high humidity (80–100 %), so that it is unlikely to give any trouble outside the forcing house. Even there it is, with rare exceptions, of minor importance, and its appearance is probably not noticed by many growers.

When conditions are favourable spore masses may be formed on the spots on the leaves in the greenhouses, and form a ready means of identifying the disease. When spores are not present the spots might easily be mistaken for those produced by fire, but they are less conspicuous and generally less numerous, and are not found on the flowers.

Inoculation experiments have confirmed the importance of high temperature and humidity. In March 1931 detached tulip shoots were kept in jars and the uninjured surface smeared with spores. Small spots appeared in about eight days, while the controls remained healthy. On the lesions spores developed five days later, from which the fungus was reisolated. The jars were maintained at different degrees of humidity and the decay extended most rapidly in the chamber which was kept thoroughly saturated. Inoculations of the variety Farncombe Sanders in pots under bell jars using spore suspensions failed completely in the open air and in an experimental greenhouse, in which the air was rather dry, spots appeared on the leaves in one pot only. Inoculations in another season in the same greenhouse by placing agar, bearing mycelium, on the soil or in contact with the shoots, failed to produce any sign of the disease.

It has been observed that the disease is particularly likely to occur where straw has been used to cover the boxes during the "rooting" period. Further, the resemblance in pure culture of several isolations from tulip foliage to strains of *F. herbarum*, which had been isolated from diseased cereal plants, led to these isolates (subsequently kindly identified by Wollenweber as belonging to the tulip form now placed under *F. avenaceum*) being tested by Dr G. W. Padwick on cereal seedlings. The cultures obtained from tulip proved to be very highly pathogenic to wheat.

It has been noted that, as a measure of false economy, growers frequently use the same straw for covering their bulbs for several seasons. Dr F. T. Bennett (*in litt.*) has confirmed the opinion that the fungus would increase, probably abundantly, on the straw year by year. It would persist readily in the dry straw during the summer, and resume saprophytic growth under the moist conditions over the boxes.

Other species of *Fusarium* have been found on tulips, especially on the bulbs, but *F. avenaceum* is probably the commonest on the foliage. It is a fungus widely distributed on many hosts, so that it is likely to be present in most nurseries. The most practical control measures

would appear to be the use of clean straw for covering the boxes out of doors, and the correct regulation of temperature and humidity (including watering) during forcing operations.

The writers wish to thank Mr W. C. Moore of the Ministry of Agriculture's Plant Pathological Laboratory, Harpenden, for references to the older literature.

REFERENCES

Höstermann, G. (1926). *Landw. Jb.* LXIV, 65.
Ministry of Agriculture (1928–32). *Fungus and other Diseases of Crops*, p. 105.
Oudemans, C. A. (1919). *Systema Fungorum*, I, 1145.
Pape, H. (1936). *Krankheiten und Schädlinge der Zierpflanzen*, 2nd ed. p. 390. Berlin.
Wollenweber, H. W. & Reinking, O. A. (1935). *Die Fusarien*, p. 293. Berlin.

STUDIES ON BRITISH PYRENOMYCETES

II. A COMPARATIVE STUDY OF *MELANOMMA PULVIS-PYRIUS* (PERS.) FUCKEL, *MELANOMMA FUSCIDULUM* SACC. AND *THYRIDARIA RUBRO-NOTATA* (B. & BR.) SACC.

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(With Plates VI and VII and 5 Text-figures)

Introduction

The genus *Melanomma* Nitschke, in Fuckel, *Symbolae Mycologicae* (1869), 159, was erected to include small, carbonaceous Pyrenomycetes, having: "Sporen meist 2–3 mal septirt, selten ohne Scheidewand, braun oder wasserhell." Eight species were described in the following order:

(1) *M. pomiformis* (Pers.) Nits. *in litt. Sphaeria pomiformis* Pers. *Syn.* (1801), 65.

(2) *M. Aspergrenii* (Fr.) Fuckel, *Sphaeria Aspergrenii* Fr. in Kze, *Myc. Hgt.* II, 40. *Syst. Myc.* II (1823), 465.

(3) *M. ovoidea* (Fr.) Fuckel, *Sphaeria ovoidea* Fr. *Syst. Myc.* II (1823) 459.

(4) *M. papillata* Fuckel, *Symb. Myc.* (1869), 159 (unter *Sphaeria ovoidea* Fr.? *Fung. Rhen.* 2166).

(5) *M. Pulvis-pyrius* (Pers.) Fuckel, *Sphaeria Pulvis-pyrius* Pers. *Syn.* (1801), 86.

(6) *M. conica* Fuckel, *Symb. Myc.* (1869), 160.

(7) *M. subsparsum* Fuckel, *Symb. Myc.* (1869), 160.

(8) *M. vile* (Fr.) Fuckel, *Sphaeria vilis* Fr. *Syst. Myc.* II (1823), 466.

Saccardo (1878*b*, p. 344) grouped these species into separate genera characterized by the colour and shape of the ascospores and emended the description of the genus *Melanomma* to read: "Spores ovate or oblong, multiseptate, coloured." He included in this genus species numbered 2, 5, 7 and 8 in the list given above and placed *M. Pulvis-pyrius* (Pers.) Fuckel as the first species. He erected a new genus *Zignoella* (named after A. de Zigno) to include species with "Hyaline ovate or oblong, multi-septate or multi-guttulate ascospores", and

placed here the species numbered 3, 4 and 6 in the list. *Melanomma pomiformis* (Pers.) Nits., which he transferred to the genus *Melanopsamma* Niessel (*Notiz über Pyren.* p. 40), has hyaline, bicellular ascospores. Since then it has been recognized as the effective type species of this genus. Later (1883, p. 98), Saccardo gave an extended description of the genus *Melanomma* which reads: "Perithecia gregarious, seldom scattered, somewhat superficial, spherical, papillate or blunt, carbonaceous, smooth or somewhat hairy. Asci elongate, for the most part accompanied by paraphyses, eight-spored. Spores oblong or somewhat spindle-shaped, two to many septate, olive coloured or dark brown. Species of *Sphaeria* de Not. and Karst. belong here for the most part." Although not the original type species of the genus *Melanomma* Nits., *M. Pulvis-pyrius* (Pers.) Fuckel has been tacitly recognized as the effective type.

M. fuscidulum Sacc. was first published by Saccardo as *Sphaeria fuscidula* (sp.nov.) f. *Sambuci nigrae* in Mycotheca Veneta specimen no. 159 and transferred (1878*c*, p. 450) to *Melanomma*. The authentic material was collected on *Sambucus nigra*.

The genus *Thyridaria* Sacc. in *Grevillea*, IV (1875), 21, has as its type species *T. incrustans* Sacc. which is not known from Britain. *T. rubronotata* was published as *Melogramma rubro-notatum* B. & Br. in *Ann. Mag. Nat. Hist.* Ser. 3, III (1859), 375, no. 894, with the description: "Perithecia confluent; ostiolum papilliform, perforated, the perforation surrounded with a brick-red meal; asci linear, sporidia uniseriate, oblong, ·0006 inch long, triseptate." It was collected on elm bark.

These three species have, in common, triseptate dark-coloured ascospores (phaeophragmospores).

The purpose of the present study is twofold. First, to investigate the development of the imperfect stage of each species in culture and to demonstrate the relationship between such stages and three species of the Fungi Imperfecti already described; second, to investigate the structure and development of the ascocarp in these species.

Imperfect stages have already been suggested by Saccardo for *Melanomma Pulvis-pyrius* (1878*c*, p. 450); *M. fuscidulum* (1881, p. 271), and *Thyridaria rubro-notata* (1883, p. 141), and Brefeld (1891, p. 201) obtained pycnidia in cultures started from ascospores of *Melanomma Pulvis-pyrius*.

M. Pulvis-pyrius and *M. fuscidulum*, as well as certain species of *Leptosphaeria*, are apparently simple perithecial forms. Within recent years, Von Höhnel, Petrak (1924) and Theissen & Sydow (1918) have shown that many species which have hitherto been regarded as simple Pyrenomycetes are in reality allied to the Dothideales rather than to the Sphaeriales. Their ascocarp is an unilocular stroma and not a perithecium. The difference is one of development. Species

belonging to the simple Sphaeriales have perithecia which develop from an archicarp (usually within a very minute stroma). The archicarp produces the whole of the perithecium; wall, ascogenous hyphae, paraphyses and periphyses. The ascocarps of species showing a dothideaceous development commence as small stromata within which an archicarp gives rise to ascogenous hyphae and asci. Paraphyses and periphyses are never produced. Although Petrak (1924) cites species of *Melanomma* as having this type of development he considers that they have true paraphyses. Miller (1928*a*) has shown that Petrak (1924) applies the term "paraphyses" to remnants of the stromatic tissue into which the asci have grown, and that he describes as "pseudo-paraphyses" the structures which other authors consider to be paraphyses (e.g. such as occur in the Xylariaceae). The recognition of species having an ascocarp with a pseudo-parenchymatous centrum and a dothideaceous type of development is of considerable importance to anyone investigating the phylogeny of the Pyrenomycetes. In view of Petrak's statement regarding a species of *Melanomma*, it was considered desirable to investigate the development of the ascocarp* in *M. Pulvis-pyrius* and to compare it with that of *M. fuscidulum* and *Thyridaria rubro-notata* and with that of species already known to have a dothideaceous type of development.

The systematic position adopted in this study is summarized below.

Melanomma Nits. in Fuckel *Symb. Myc.* (1869), 159.

(1) *M. Pulvis-pyrius* (Pers.) Fuckel, *loc. cit.*
Syn. *Sphaeria Pulvis-pyrius* Pers. *Syn. Fung.* (1801), 86.
S. myriocarpa Berk., *F. North Amer.*
S. conglobata Fr., *Syst. Myc.* II (1823), 414.
M. subsparsum Fuckel, *Symb. Myc.* (1869), 160.

(2) *M. fuscidulum* Sacc., in *Hedw.* XIV (1875), nos. 5 and 45; *Mich.* I (1878), 450.
Syn. *Sphaeria fuscidula* Sacc., f. *Sambuci nigrae* Sacc. *Myc. Ven.* II (1873), no. 159.

Thyridaria Sacc. in *Grevill.* IV (1875), 21.

T. rubro-notata (B. & Br.) Sacc., *Syll.* II (1883), 141.
Syn. *Melogramma rubro-notatum* B. & Br. in *Ann. Mag. Nat. Hist.* Ser. 3, III (1859), 375, no. 894.
Massaria lateritia Tul., *Sel. Fung. Carp.* II (1863), 243.
T. delogensis Speg. & Roum., in *Rev. Myc.* II, 21.

* In the course of this study the word perithecium is used merely for convenience and because the ascocarp of *Melanomma Pulvis-pyrius* has for so long been recognized as a simple perithecium.

Table I. *Type specimen and certain other collections of* Melanomma Pulvis-pyrius

Source exsicc.	No.	Host	Asci μ	Ascospores μ
Fung. Rhen.	937	—	Too few for exact measurements	11·5–16 × 4–5
Mason	222	*Acer*	—	14–17 × 4–5
,,	223	,,	84–106 × 7–8	14–16 × 4–5
,,	343	*Betula*	96–113 × 6–8	13–16 × 4–5
,,	342	,,	86–116 × 6–7	12–17 × 5
,,	345	,,	87–102 × 6–7	14–16 × 4–5
Chesters	52*	,,	90– 96 × 7–8	14–18 × 4–6
Mason	413	*Corylus*	—	14–16 × 4–5
,,	415	,,	84–131 × 5–7	14 × 4–5
,,	416	,,	—	13–17 × 4–5
,,	483	,,	—	14–16 × 5
Chesters	53*	,,	85– 99 × 6–7	14–16 × 5–6
,,	206*	,,	87–110 × 6–8	14–15 × 5
Mason	1275*	*Carpinus*	96–116 × 6–7	14–18 × 4–5
,,	612	*Fagus*	88–120 × 6–7	15–18 × 4–6
,,	611	,,	—	13–16 × 5–6
,,	1269	,,	—	14–17 × 4–6
Chesters	24*	,,	97–106 × 6–7	14–16 × 4–5
,,	351*	,,	—	15–16 × 5–6
J. Ehrlich	1500*	,,	—	14–16 × 4–6
Mason	731	*Fraxinus*	96–119 × 6–8	14–16 × 4–6
,,	730	,,	68– 94 × 6–8	13–15 × 4–5
,,	729	,,	93–112 × 6–7	14–18 × 4–5
,,	767	*Ilex*	100–103 × 5–6	13–15 × 4–5
,,	1225*	,,	92–106 × 6–7	12–15 × 4–5
Chesters	13*	*Populus*	80–100 × 6–7	14–15 × 4–6
,,	10*	*Pyrus*	91– 99 × 6–7	14–16 × 4–6
Mason	895	*Rhamnus*	92–103 × 6–7	15–16 × 4–6
Chesters	347*	*Tilia*	96–110 × 6–7	14–15 × 4–5
Mason	990	*Ulex*	76– 85 × 5–8	14–17 × 4–6
,,	1061	*Ulmus*	—	14–17 × 4–5
,,	1063	,,	—	15–17 × 5–6
,,	1066	,,	100–116 × 6–7	14–16 × 4–5
Chesters	198*	,,	94–112 × 6–7	14–16 × 4–6

* Have been isolated.

II. Comparison of material* on which this study is based with authentic material

(1) *Melanomma Pulvis-pyrius* (Pers.) Fuckel

Type: Fuckel, *Fungi Rhenani*, No. 937. The specimen examined is in the Herbarium of the Royal Botanic Gardens, Kew.

Fuckel's exsiccatum consists of gregarious, superficial perithecia which are subspherical, scarcely ever beaked and somewhat rugose. They contain spindle-shaped, light brownish, triseptate ascospores

* The cultural work of this study is based on collections lodged either in the herbarium of Mr E. W. Mason or in my own. Reference will be made to such specimens as are necessary for the discussion by means of the numbers attached to the specimens in these herbaria.

(vide Table I). Their characteristic shape is due to the fact that the equatorial septum which is the first to appear, divides the spore into a wider anterior part and a narrower posterior part; each of these parts later develops a single transverse septum (Text-fig. 1 A). The spore shape is of importance. It is also characteristic of *Melanomma fuscidulum* and differentiates ascospores of these species from the brown, triseptate ascospores of certain species of *Leptosphaeria*. In all spore measurements given in Table I the breadth figure refers to the widest part of the anterior portion of the spore which in Fuckel's collection, and in all others examined, may be 1–1·5 μ greater than the widest part of the posterior portion.

The ascospore size varies slightly in every collection whether from the same or from different host substrates. The range for the collections examined is 11·5–18 × 4–6 μ; the usual measurements of most of the spores being 14–16 × 5 μ. These do not agree with the figures given by Saccardo (1878*c*, p. 450) which all indicate spores of greater length. On *Ulmus*, Saccardo (1878*c*) reports spores with four or five transverse septa and very occasionally with one or two longitudinal septa, but I have never observed any departure from the triseptate condition although I have examined many collections on this host.

The ascus (Text-fig. 1 A–D) is cylindrical with a short, scarcely tapering stalk ending in a rather broad base. At the apex the wall is rounded or dome-shaped and somewhat thickened and has usually

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Legend to Text-figure 1.

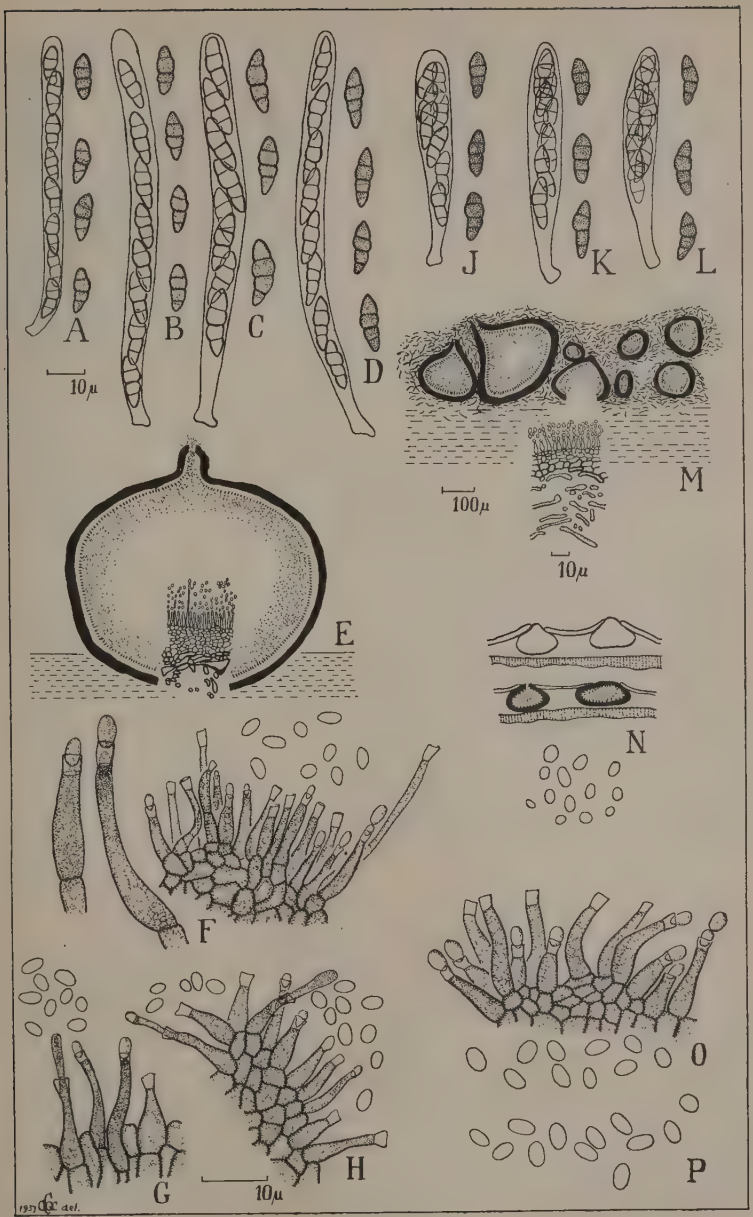
A–H. *Melanomma Pulvis-pyrius* (Pers.) Fuckel

A. Ascus and ascospores from the type collection, *Fung. Rhem.* 937.
B. Ascus and ascospores from a collection on *Corylus*.
C. Ascus and ascospores from a collection on *Betula*.
D. Ascus and ascospores from a collection on *Ulmus*.
E. Median section of a pycnidium showing details of wall structure.
F. Phialides and phialospores from a pycnidium developed in a culture isolated from *Ilex* (the two drawings on the extreme left are greatly enlarged to show the mode of production of the conidia).
G. Similar structures from a pycnidium collected on *Ulmus*.
H. Phialides and phialospores from a pycnidium developed in a single ascospore culture from *Ulmus*.

J–P. *Melanomma fuscidulum* Sacc.

J. Ascus and ascospores from the type collection, *Myc. Ven.* 159.
K. Ascus and ascospores from a collection on *Fagus*.
L. Ascus and ascospores from a collection on *Ulmus*.
M. Longitudinal section through several pycnidia immersed in a coarse mycelial byssus. Detailed structure of the wall of one pycnidium is shown.
N. Figures illustrating the form and arrangement of the pycnidia of *Coniothyrium fuscidulum* and the shape of its conidia (after Berlese).
O. Phialides and phialospores from a pycnidium developed in a culture isolated from Fagus.
P. Phialospores from a pycnidium collected on *Ulmus*.

(The scale of the drawings A–D and J–L is shown under A, that of E and M under M and that of F–H and O–P under H.)



Text-fig. 1.

a rather clearly marked central pore. The ascospores are monostichous both in the young and the mature ascus. It sometimes happens that a few asci from certain collections have subdistichous ascospores but these never approach the regular distichous arrangement of the ascospores of *Melanomma fuscidulum* (Text-fig. 1 J–L).

The "paraphyses" will be dealt with more fully in a later section but it must be emphasized that these persistent, septate filaments are branched and frequently anastomose (Text-fig. 3 A). If a young perithecium is carefully opened it is possible to excise the hyaline central portion from the carbonaceous wall and by pressing flat these softer tissues to demonstrate that the "paraphyses" are continuous, from the ventral ascus-bearing stratum to the dorsal tissue through which dehiscence will later occur. They are plentiful even in fully mature perithecia and always retain their characteristic structure.

Although the perithecia arise within the upper layers of the wood or below the periderm they are erumpent at so early a stage that the mature fruit body appears superficial (Pl. VI, fig. 1). They are generally densely aggregated in crowded groups (i.e. the state of *Sphaeria conglobata* Fr.) or in a black crust and seldom occur as scattered individuals. Their shape is diverse, varying from the compressed rugose and sulcate type of the crustose state to the sphaeroid, papillate or multirostrate and smoother surfaced type of the more widely separated state. But each condition, and many intermediate states, may be seen in a single collection (Pl. VI, fig. 1). The papillate types are frequently characteristic of a damper habitat. The actual point of dehiscence may be quite removed from the apex of the papilla but is always in the dorsal hemisphere of the perithecium. The size of mature perithecia, while variable, falls within the range 210–460 × 180–370 μ. For any single collection the usual size may vary within 100 or 200 μ and no characteristic value can be assigned to perithecia from any one host.

(2) *Melanomma fuscidulum* Sacc.

Type. Saccardo, *Mycotheca Veneta*, specimen No. 159. The material examined is in the Herbarium of the Royal Botanic Gardens, Kew.

Saccardo's collection in *Mycotheca Veneta* consists of scattered, beaked, rugulose perithecia partly immersed in the decaying wood of *Sambucus* (Pl. VII, fig. 1). The venter of the perithecium is globular and tapers gradually to a cylindrical or more often conical neck widely fractured across the apex in mature perithecia. The asci are cylindrical-clavate with rather broad short pedicels (Text-fig. 1 J). "Paraphyses" of similar character to those of *Melanomma Pulvis-pyrius*

Table II. *Type specimen and certain other collections of* Melanomma fuscidulum

Source	exsicc.	Asci μ	Ascospores μ
Myc. Ven.	No. 159, in Herb. Kew.	Not sufficient for determination	12–14 × 3–4
Ibid., but in *Herb. Myc.*, M. C. Cooke		—	11–14 × 3–4
Mason	No. 1226*, on *Fraxinus*	52– 60 × 9	12–16 × 4–4·5
Mason	No. 1292*, on *Fagus*	68–101 × 6–8	12–16 × 3–4
Chesters	No. 348*, on *Fagus*	54– 69 × 6–7	12–14 × 4
Mason	No. 934, on *Sambucus*	46– 56 × 8–10	13–16 × 4
Chesters	No. 494*, on *Sambucus*	50– 60 × 6–8	13–15 × 4
Chesters	No. 374*, on *Ulmus*	60– 68 × 9–10	14–16 × 4

* Have been isolated.

are present. The ascospores (vide Table II) are regularly biseriate (Text-fig. 1 J) and are slightly shorter, narrower and of a darker colour (olivaceous-fuliginous) than those of *M. Pulvis-pyrius*.

Certain important characteristics emerge from an examination of British collections on *Fraxinus*, *Fagus*, *Sambucus* and *Ulmus*. The perithecia may be erumpent in groups through the periderm (as in *Fagus*—Pl. VI, fig. 2) or evenly scattered and semi-immersed in the decayed upper layers of the wood (as in decorticated *Fraxinus* and *Ulmus*). On hard, dry wood (e.g. of *Ulmus*) they may be densely crowded and frequently, apparently entirely superficial. Whatever the condition of the mature perithecium it always originates within the host tissues and beneath a felt-like layer of olivaceous to brownish olivaceous mycelium through which it grows and by which the base of the venter is finally surrounded. This mycelial byssus can always be discovered either by dissecting away the periderm or closely examining the decorticated wood. The pycnidial stage of the fungus may be collected below this felt of mycelium. The length of the perithecial neck is subject to considerable variation. It is shorter and broader when the perithecium is immersed and more narrowly cylindrical when the perithecium is fully erumpent through the periderm or the wood. One collection on *Ulmus* (no. 374) bore perithecia within a knot-hole in the wood which had much longer and more narrowly cylindrical necks than those of superficial perithecia. Such abnormally long necks are probably due to a high atmospheric humidity in such a practically enclosed space.

There is extremely close correspondence between the asci and ascospores of the collected material and those of the authentic material (vide Table II and Text-fig. 1 J–L). The habitat of this fungus is more restricted than that of *Melanomma Pulvis-pyrius*, since the perithecia occur on fallen wood lying in relatively damp situa-

tions. It is not a fungus of first incidence and frequently occurs along with species of *Zignoella*, *Trichosphaeria myriocarpa* and species of *Ceratostomella* (sensu Saccardo).

(3) *Thyridaria rubro-notata* (B. & Br.) Sacc.

Type. *Melogramma rubro-notatum* B. & Br. collected by M. J. Berkeley on *elm* bark, King's Cliffe, 24 December 1852. The material examined is in the Herbarium, Royal Botanic Gardens, Kew.

Isolations were made from specimens collected on *Ulmus* in the grounds of the Imperial Mycological Institute, Kew, and from a specimen on *Acer* collected by Mr F. J. Rilstone and sent to Mr W. B. Grove, to both of whom I am much indebted for the use of this material.

The type collection and the two collections from which isolations have been made are similar in character. They bear erumpent pustules of perithecia surrounded by closely adhering periderm. These pustules may contain only the ascophorous or the pycnidial state or both together (Pl. VI, fig. 3). The black perithecia have a spherical venter extending upwards into a short, broad neck perforated, when mature, by a clearly defined pore. The several perithecia of a pustule are embedded in a mycelial plexus consisting of closely interwoven thick-walled, brown hyphae. Reddish hyphae extend from this plexus over the young perithecia and later break up into segments which, in mass, produce the red meal that gives the specific epithet to the species. This meal also surrounds the pycnidia. The mycelial plexus extends between the wood and cortex from one pustule to another. A discussion on the precise nature of this plexus and its bearing on the taxonomic position of the species will be deferred to a later section.

The asci of the type material on *Ulmus* and of the collected material on *Ulmus* and *Acer* are cylindrical with a short slightly tapered stalk (Text-fig. 2 A–C). They contain monostichously arranged dark brown, triseptate ascospores (vide Table III).

Table III. *Type specimens and other collections of* Thyridaria rubro-notata *and* T. delognensis

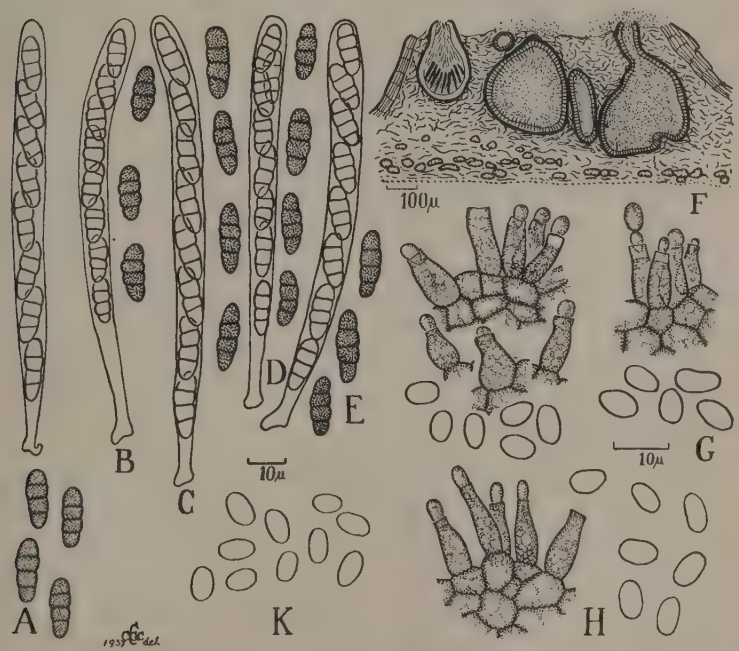
Source	Asci μ	Ascospores μ
T. rubro-notata (B. & Br.) Sacc		
Type: on *Ulmus*, King's Cliffe, 24 December 1852	110–117 × 8–9	15–17 × 6
Exsicc. Chesters, No. 27*, on *Ulmus*	100–120 × 7–10	14–19 × 5–6
Exsicc. Chesters, No. 550*, on *Acer*	100–120 × 8	16–18(20) × 5–6
T. delognensis Speg. & Roum.		
Type: *Fungi Gall. exsicc.*, No. 2686 on *Acer*,	90–115 × 6·5–7	14–16 × 5–6
Sydow: *Myc. Marchica*, No. 3040, on *Fraxinus*	100–128 × 7–8	14–16 × 5–6

* Isolated in culture.

(4) *Thyridaria delognensis* Speg. & Roum.

Type. Roumeguère, *Fungi Gallici exsiccati*, no. 2686.

The specimen examined is in the Herbarium of the Royal Botanic Gardens, Kew. The perithecia are not so liberally covered with the red farina as are those of the type collection of *T. rubro-notata*, but in other respects they agree. Most of the perithecia have young asci and a few have mature ascospores, but sufficient mature asci and



Text-fig. 2. *Thyridaria rubro-notata* (B. & Br.) Sacc.

A. Ascus and ascospores from the type specimen collected by M. J. Berkeley on *Ulmus*, King's Cliffe, 24 December 1852.
B. Ascus and ascospores from a collection on *Ulmus*.
C. Ascus and ascospores from a collection on *Acer*.
D. Ascus and ascospores from the type collection of *T. delognensis*, Fung. Gall. 2686.
E. Ascus and ascospores from *Myc. March.* 3040.
F. Longitudinal section through a pustule, containing pycnidia and one perithecium, collected on *Ulmus*.
G. Phialides and phialospores from pycnidia, those on the right being from a collection on *Ulmus*, those on the left from a culture isolated from that host.
H. Phialides and phialospores from a pycnidium collected on *Acer*.
K. Phialospores from a culture isolated from *Acer*.

(The scale of the drawings A–E is shown under D, that of G–H under G.)

ascospores are present to show that they agree precisely in shape, size and colour with those of the type material of *T. rubro-notata* (vide Table III and cf. Text-fig. 2 D with Text-fig. 2 A).

T. delognensis Speg. & Roum. must be regarded as a synonym of *T. rubro-notata* (B. & Br.) Sacc.

Specimen no. 3040 in Sydow's *Mycotheca Marchica* is referred to *T. delognensis*. The host is *Fraxinus*. This specimen was examined at the herbarium of the British Museum and of the Royal Botanic Gardens, Kew. It possesses perithecia, asci and ascospores exactly comparable with those of the type collection of *T. rubro-notata* (vide Table III and Text-fig. 2 E) and should therefore be placed under that species as a new host record.

III. The life histories

(*a*) *The conidial stage*

The cultures used in this study were started from single ascospores and from groups of ascospores discharged from freshly collected, mature perithecia. The spores were collected on clear malt agar plates inverted over the ripe perithecia. Such spores germinate more rapidly than those excised from perithecia. Subcultures from monospore and multispore isolations were grown on a range of media including malt, Leonian's, oat, maize extract and lentil extract agar. Cultures on slopes of agar in medicine bottles proved highly satisfactory as the large volume of pabulum and freedom from contamination allowed continuous observation for periods exceeding six months. Both sterilized and fresh host tissues were inoculated with subcultures of all isolations. The latter were the most satisfactory and, with the exception of the isolations from *Melanomma fuscidulum*, allowed the species to complete their full life cycle. The fresh host branches were swabbed with 95 % alcohol, air dried, reswabbed and the excess alcohol flamed off; they were then inoculated by inserting the end of the surface-sterilized branch into a vigorous culture of the fungus. Once mycelial growth was well established the inoculated branch was removed to a sterile tube containing sterile moist sand and after a further period of incubation at room temperature was transferred out of doors. In all experiments with *Melanomma Pulvis-pyrius* and *Thyridaria rubro-notata*, perithecia were eventually obtained upon any host wood which was inoculated irrespective of the host from which the inoculum was originally obtained.

(1) *Melanomma Pulvis-pyrius.*

Saccardo considered *Phoma Pulvis-pyrius* Sacc. (1878*c*, p. 450) to be the pycnidial stage of this species and described the pycnidia as somewhat similar to but not so large as the perithecia, containing

small, cylindrical, hyaline conidia, $3–4 \times 0{\cdot}75\,\mu$, arising from the apices of much branched sporophores. This is the fungus which he later called *Dendrophoma Pulvis-pyrius* Sacc. (*Fung. Ven. Nov.* Ser. 3, no. 18). Monospore isolations from a collection received from Mr E. W. Mason which was almost certainly referable to this species gave cultures differing both in their gross characters and in the dendroid sporophores of the pycnidia from the cultures obtained from ascospores of *Melanomma Pulvis-pyrius*. There is little reason to suppose that *Phoma Pulvis-pyrius* Sacc. has anything to do with the life cycle of *Melanomma Pulvis-pyrius*.

Brefeld (1891, p. 201) obtained rod-shaped, straight or slightly curved, hyaline conidia $4–5 \times 1{\cdot}5\,\mu$ from pycnidia produced in cultures started from ascospores of *M. Pulvis-pyrius*. The conidia observed in the isolations prepared during the present study do not agree in shape or size with those described by Brefeld.

The first isolations of *M. Pulvis-pyrius* were obtained during 1932 and 1933 from a collection made by Mr E. W. Mason on *Ilex* (no. 1225). They produced a greyish green, stiffly flocculent mycelium limited by a greenish fawn or dirty cream coloured margin. Numerous small, somewhat papillate, black carbonaceous pycnidia excreting a copious cream-coloured mass of hyaline conidia developed amongst the aerial hyphae over the superficial mat of mycelium (Pl. VII, fig. 2). The conidia were cylindrical to ovoid, blunt at both ends, $2–3{\cdot}5 \times 1{\cdot}5–2\,\mu$ and contained two, almost polar, guttules. The pycnidia were clearly to be referred to an affinity near to *Phoma* but a precise specific identification on cultural characters alone seemed utterly useless, since the published species of this affinity are described from specimens occurring in nature upon definite substrates. Very few species have ever been grown in culture and those which have are not known sufficiently to allow of accurate comparison and identification. While it is not even certain that the species described from different host plants in nature are distinct, it would be ridiculous to assign a name based on the features of a fungus growing on a plant substrate to a culture growing on laboratory media, even though characteristics of comparable taxonomic value could be discovered. Therefore an attempt was made to collect a pycnidial stage in association with the perithecia of the species in nature, to obtain cultures from single conidia and to compare such cultures with those from ascospores of the associated perithecia. Collections during 1933 and 1934 did not yield such material, although isolations did give cultures comparable with those already obtained from *Ilex* and bore similar *Phoma*-like pycnidia. In January 1935 numerous perithecia were collected on dry, decorticated wood of *Ulmus*, and pycnidia were discovered at one end of the branch (Pl. VII, fig. 4). The pycnidia were superficial, smooth, black, sphaeroid or spherical and shortly papillate

or with two or three short beaks. The conidia were extruded in a cream-coloured mass and were ellipsoid or oblong, rounded at both ends, hyaline, biguttulate and $2{\cdot}5–3 \times 2\,\mu$ and developed from the ends of simple flask-shaped sporophores about $15\,\mu$ in length.

Cultures were established from single ascospores and conidia which produced identical mycelia on a wide range of media (Pl. VII, figs. 3 and 5). The pycnidia and conidia of these cultures were indistinguishable from one another and from those of all other cultures of *Melanomma Pulvis-pyrius* (vide Table IV).

Table IV. *Measurements of the conidia of* Melanomma Pulvis-pyrius, M. fuscidulum *and* Thyridaria rubro-notata

No.	Material	Conidia μ
	M. Pulvis-pyrius	
198 A	Collected on *Ulmus*	2–3·5 × 1·5–2·5
198 A	From cultures from single conidia	2·5–3·5 × 1·5–2
198	From cultures from ascospores	2–3 × 1·5–2
10	,, ,, ,, ,,	2–3·5 × 1·5–2+
13	,, ,, ,, ,,	2+–3·5 × 1·5–2·5
24	,, ,, ,, ,,	2·5–3·5 × 1·5–2
52	,, ,, ,, ,,	2–2·5 × 1·5–2
206	,, ,, ,, ,,	2+–3·5 × 2–2+
1225	,, ,, ,, ,,	2–3·5 × 1·5–2
351	,, ,, ,, ,,	2·5–3 × 1·5–2·5
347	,, ,, ,, ,,	2+–3·5 × 1·5–2·5
1550	,, ,, ,, ,,	2·5–3·5 × 1·5–2
1275	,, ,, ,, ,,	2·5–3 × 1·5–2
	M. fuscidulum	
374	Collected on *Ulmus*	3·5–5 × 2·5–3
374	From cultures from single conidia	4 –5 × 2 –3
374	From cultures from ascospores	3·5–4·5 × 2·5–3
1226	,, ,, ,, ,,	3·5–4 × 2·5–3
1229	,, ,, ,, ,,	3·5–4 × 2·5–3
494	,, ,, ,, ,,	3·5–5 × 2+–3
	T. rubro-notata	
27	Collected on *Ulmus*	5–8 × 3–4
550	,, ,, *Acer*	3–8 × 3–5
	Fung. Gall. 2686	5–6 × 4

The pycnidial wall consists of an outer zone of four to six layers of dark brown thick-walled cells enclosing a pseudo-parenchymatous layer of hyaline cells. Simple sporophores project from the inner surface of this layer to form a zone lining the pycnidial cavity (Text-fig. 1 E). These sporophores are flask-shaped phialides (1933, p. 8). The apex enlarges as a small collar surrounding the active growing point from which the several serial phialospores are produced (Text-fig. 1 F). Whether the phialospores adhere in chains depends upon the physical conditions existing within the pycnidium. This description refers to pycnidia on malt agar developed from ascospores of collection no.

1225, but it applies equally to the pycnidia developed from the conidia of collection no. 198 A. The phialides and phialospores of the pycnidia on *Ulmus* (Text-fig. 1 G) are exactly similar to those of pycnidia in culture (Text-fig. 1 H). It is of interest to notice that the phialide may proliferate and form beyond the original collar a secondary phialide which continues to produce phialospores (Text-fig. 1 G). The apex of the young phialide is rounded and the collar is evident only after the first spore has been shed. The collars collapse when pycnidia are placed in fixing solutions and are not usually seen in microtome sections. They are best displayed by staining sections, cut with the freezing microtome, in 1 % aqueous congo red and mounting them in water. From observations of a number of other fungi it is believed that all phialides producing slimy phialospores possess such collars.

The pycnidia collected on *Ulmus* may be described as: scattered or crowded together in small groups, superficial or immersed round the base but never totally immersed in the substratum, globose-conical, about 200–300 μ in diameter (occasionally up to 800 μ in diameter—then somewhat pseudolocellate), black, carbonaceous, shortly papillate; conidia (phialospores) hyaline, ellipsoid or somewhat oblong, rounded at each end, biguttulate, $2–3{\cdot}5 \times 1{\cdot}5–2{\cdot}5\,\mu$, arising from flask-shaped sporophores (phialides). These characters suggest an affinity with species of *Aposphaeria* Berk. which differ from species of *Phoma* in the fact that the pycnidia are never completely immersed in the host tissues. They occur on the surface both of bark and of wood and are usually papillate, globose or irregular in shape, pseudoparenchymatous in texture and carbonaceous. Of the species which occur on hardwood trees *Aposphaeria agminalis* Sacc. *Syll.* III (1884), 171 (*Phoma agminalis* Sacc. in *Mich.* II (1881), 379) appears, by description alone, to agree most closely with the imperfect stage of *Melanomma Pulvis-pyrius* as it was collected on *Ulmus*. Saccardo describes this species as follows: "Pycnidia scattered or clustered into groups, almost superficial, punctiform, globose-conical, shining-black, 90–100 μ in diameter; spores ellipsoid, obtuse at both ends, biguttulate, hyaline, $3 \times 2\,\mu$. On hard wood of *Aesculus Hippocastanus*." He suggests that it may be the conidial stage of a *Zignoella*. While absolute proof of the identity of *Aposphaeria agminalis* with the fungus on *Ulmus*, and hence the imperfect stage of *Melanomma Pulvis-pyrius*, cannot be obtained without examining authentic material there is every reason to believe that the name is correctly assigned. Mr W. B. Grove has kindly examined my specimen and writes (*in litt.*): "I think 198 A is so very like *Aposphaeria agminalis* that it cannot be named anything else until one can actually compare it with Saccardo's own specimen." Mr Grove considers *Aposphaeria ulmicola* Sacc. = *Phoma ulmicola* Berk. (in Hook. *J. Bot. Kew*, XL (1853) (see infra, p. 134) to be merely an

immature state of *A. agminalis* Sacc.: the description given by Grove (1935, p. 140) certainly suggests this to be so. The following species of *Aposphaeria* are described with characters so similar to *A. agminalis* as to raise grave doubt that they are specifically distinct:

On *Betula.*	*A. cruenta* Vestergr. in *Oefv. K. Vet. Akad. Förhahal.* No. I (1897), 38.
„ *Betula.*	*A. nigra* Died. in *Krypt. Mark Brand.* IX (1915), 201.
„ *Carpinus.*	*A. rugulosa* Sacc. in *Giorn. bot. ital.* VIII (1876), 179.
„ *Corylus.*	*A. subtilis* (Fr.) Sacc. *Syll.* III (1884), 171. Syn. *Sphaeronema subtilis* Fr. in Kunze u. Schmidt, *Mycol. Hefte*, II, 57.
„ *Fagus.*	*A. freticola* Speg. *Fung. Pat.* No. 16.
„ *Ilex.*	*A. Ilicis* Died. in *Krypt. Mark Brand.* IX (1915), 205.
„ *Salix.*	*A. gregaria* Died. in *Krypt. Mark Brand.* IX (1915), 207.
„ *Tilia.*	*A. difformis* Sacc. *Syll.* III, 172. Syn. *Phoma difformis* Sacc. in *Mich.* I (Jan. 1878), 125.

It has been impossible to examine type material of these species, but the essential diagnostic characters are set out in Table V and compared with those of *A. agminalis* and with those of the pycnidia collected on *Ulmus*.

(2) *Melanomma fuscidulum* Sacc.

Saccardo assigned *Phoma fuscidula* Sacc. (1881, p. 271) to this species as its pycnidial state describing it as: "Pycnidia gregarious with their base slightly embedded in the host wood, globose-conical, with a very small beak, black; conidia oblong, obtusely rounded at each end, $3–4 \times 1{\cdot}5–2\,\mu$, biguttulate, at first hyaline later slightly yellowish. On decorticated branches of *Sambucus nigra*." Later (1884, p. 173) he transferred the species to *Aposphaeria* as *A. fuscidula* Sacc. Previously (1878*a*, p. 205) he had described *Coniothyrium fuscidulum* Sacc. as: "Pycnidia gregarious, shining amongst the fibres of the wood, erumpent, globular; conidia globose-ovoid, $4–5 \times 3–4\,\mu$, uniguttulate, olivaceous. In decorticated branches of *Sambucus* associated with *Melanomma fuscidulum* Sacc., of which it seems to be the spermogonium." This species was later compiled in *Sylloge*, III, 307, but the conidia are given there as $4–5 \times 2–3{\cdot}5\,\mu$. Berlese (*Fungi Moricolae*, 1889, fasc. VI, no. 19, and Table 49, figs. 18–20) described and figured this species. His description reads: "Pycnidia gregarious, black, $\frac{1}{4}$ mm. in diameter, globose-conical, shining, furnished with a papillate neck, at first covered by the epidermis, afterwards free; spores globose or globose-ovoid, $4–5 \times 4\,\mu$, olivaceous. In dead branches of *Morus alba*" (vide Text-fig. 1 N). Diedicke (1915, p. 576) tran-

Table V. *Species of* Aposphaeria *resembling* A. agminalis *Sacc.*

Species	Essential characteristics of Pycnidia	Conidia	Sporophores
agminalis,	Globose-conical, punctiform, 90–100 μ, diam.	Ellipsoid or oblong, obtuse at both ends, hyaline, biguttulate, $3 \times 2\mu$	—
Collected on *Ulmus*	Globose-conical, neck short, 200–300 μ diam.	Ellipsoid or somewhat oblong, rounded at the ends, hyaline, biguttulate, $2–3{\cdot}5 \times 1{\cdot}5–2{\cdot}5\mu$	Simple 10–28 μ, mostly $\pm 15\mu$ in length
rugulosa	Spherical, papillate, rugose or wrinkled, rather large	Ellipsoid, hyaline, $2 \times 1{\cdot}5\mu$	—
difformis	Globose-conical or irregular, neck short, 250–300 μ diam.	Ellipsoid, hyaline, $2{\cdot}5–3 \times 2\mu$	Tufted
cruenta	Subglobose, vertex rounded or papillate, 90–120 μ diam.	Cylindrical, oblong or globose to subglobose, hyaline, $3 \times 1–3\mu$	—
freticola	Globose-conical, later collapsing, shortly papillate	Oblong, hyaline, guttulate, $2{\cdot}5 \times 1\mu$	Filiform, $\pm 20\mu$ long, $1{\cdot}5\mu$ thick
nigra	Irregular, not beaked, up to 450μ	Spherical or shortly oval, uniguttulate, hyaline, $2–3\mu$ diam.	—
gregaria	Globose, oval or irregular, not beaked, 200μ or more diam.	Oval or ellipsoid, 2 polar guttules, $3 \times 1{\cdot}5\mu$	Filiform, $10–12 \times 1{\cdot}5\mu$ clustered
ilicis	Globose or compressed, neck conical, $\pm 375\mu$ in diam.	Oblong, rounded at the ends, hyaline, $2–3 \times 1–1{\cdot}5\mu$	Filiform, straight or curved slightly, $15–25 \times 1–1{\cdot}5\mu$
salicis	Spherical, lenticular or compressed, not beaked, $\pm 120\mu$ in diam.	Oblong, rounded at the ends, biguttulate, hyaline, $2{\cdot}5 \times 0{\cdot}6\mu$	—

scribes Saccardo's description of *Coniothyrium fuscidulum*, mentioning that it is frequently found in association with *Melanomma fuscidulum* in Germany and, following Saccardo, states that it is the conidial stage of this species. He also (1915, p. 208) transcribes the description of *Aposphaeria fuscidula* and adds: "Nach Saccardo ist diese Art Spermagonienform zu *Melanomma fuscidula*." The descriptions of these two species are so nearly alike as to suggest that the fungi described are merely differing samples of the same species. Although no authentic specimens have been available for examination, it will be seen from what follows that this is almost certainly so.

The first isolations of this species were made during March 1933 from Mr E. W. Mason's collection on *Fraxinus* (no. 1226, Table II) and produced a dull brownish green, cushion-like mycelium of limited diameter. The mycelium grew very slowly even at the optimum temperature (18–20° C.) and practically ceased to grow between 25

and 28° C. Pycnidia were not observed during repeated inspections of the isolation plates or of subsequent subcultures. In September of the following year cultures were obtained from a collection on *Fagus* (no. 1292, Table II) which only differed from those of 1226 in their more bottle-green colour. At first no pycnidia were observed, but after several transfers had apparently failed to produce pycnidia the aerial mycelium of certain of the earlier subcultures was carefully removed with fine needles and a few pycnidia were disclosed on the surface of the agar. They were small, about 200–250 μ in diameter, smooth, shining-black and minutely papillate. Some had excreted yellowish cream coloured masses of oval or subglobose conidia, 3·5–4 × 2·5–3 μ in diameter. Individual spores were hyaline or faintly yellowish and either uni- or biguttulate.

The disclosure of these enveloped pycnidia in subcultures from collection no. 1292 indicated that they might equally well be present in isolations of no. 1226, but in the latter such pycnidia were only observed in subcultures on slopes of Leonian's agar. Pycnidia were never abundant in agar cultures. On sterile host wood they were few and seldom covered by such dense masses of mycelium as to hide them entirely. The pycnidia were similar in structure (Text-fig. 1 M) to those of *Melanomma Pulvis-pyrius* but contained decidedly broader phialides (Text-fig. 1 O). This must be interpreted side by side with the larger size of the phialospores (vide Table IV).

During January 1936 *Melanomma fuscidulum* was collected on *Ulmus*. The perithecia were accompanied by the usual mat of mycelium (cf. supra, p. 123, and Pl. VII, fig. 6). Closer examination showed that spherical conceptacles occurred amongst the more scattered perithecia. They lacked the long neck characteristic of the perithecia and were almost entirely covered by mycelium (Pl. VII, fig. 6). On breaking open the wall of a single conceptacle numerous hyaline, oval to subglobose conidia, 3·5–5 × 2·5–3 μ (mostly 4 × 3 μ) in size, were obtained. The pycnidia and the conidia agreed in character with pycnidia developed from ascospores of this collection and the two previously investigated (vide Table IV). Mycelia obtained from single conidia developed into cultures which were indistinguishable from single ascospore cultures. The collected pycnidia may be described as: Scattered in small groups amongst the perithecia, globose, with very minute rather dome-shaped papillae, black, carbonaceous, adnate or barely immersed in the fibres of the host wood, covered by a yellowish brown byssus of stout wiry hyphae when young, later gradually emerging and eventually becoming free except for a persistent investment round the base. Conidia frequently oblong but more often oval or subglobose, rounded at each end, hyaline, uni- or biguttulate (Text-fig. 1 P), 3·5–5 × 2·5–3 μ (almost all subglobose and 4 × 3 μ). The conidia are true phialospores

arising in series from phialides similar in all respects to those observed in the pycnidia of cultures derived from ascospores of collections 1226 and 1292 (e.g. Text-fig. 1 O and P).

Such characters correspond closely with those of *Aposphaeria fuscidula* Sacc., but since no authentic specimen has been examined the name is applied on the basis of comparison with Saccardo's description. It will be remembered (vide supra, p. 130) that the main distinction between *Aposphaeria fuscidula* and *Coniothyrium fuscidulum* lies in pigmentation of the conidia and a slight difference in the range of size of the conidia. Neither of these characters exhibits sufficient divergence to allow a precise separation into two species and I therefore propose to consider the names synonymous until an examination of type material shall indicate valid differences. Since January 1936 *Melanomma fuscidulum* has been collected frequently on hard, decorticated wood of *Ulmus* and ascospores from each collection have given mycelia resembling those derived from collections 1226, 1292 and 374. Pycnidia have never been numerous but have always been similar to the collected pycnidia and to others developed in culture.

The pycnidia of these two species of *Melanomma* resemble one another in their shape, colour and texture and most important of all in the fact that the small, simple conidia (phialospores) arise in succession from the apices of simple, unbranched sporophores which are unicellular and are typical phialides. They are considered to belong to the form genus *Aposphaeria*. The ascophorous forms to which each is related are distinct, but closely related, species and this is reflected in the details of the pycnidia. Those of *M. Pulvis-pyrius* are larger, more definitely papillate than those of *M. fuscidulum* and always free of mycelial vestment. They produce smaller, more elongate conidia from more slender sporophores. The mycelium of *M. Pulvis-pyrius* grows more rapidly than that of *M. fuscidulum* both in culture on agar media and on inoculated host tissues.

(3) *Thyridaria rubro-notata* (B. & Br.) Sacc.

There can be no dispute as to the relationship of the pycnidial state of this species to the ascophorous state since the pycnidia occur, in nature, either in contact with the perithecia or on the same mycelium that bears the perithecia. Single ascospores and single conidia produce identical cultures bearing entirely similar pycnidia. Several species of the Fungi Imperfecti have been suggested as the conidial state of this Pyrenomycete. Some of these suggestions will be reviewed and discussed. The structure of the pycnidium will be described and compared with that of the pycnidia of *Melanomma Pulvis-pyrius* and *M. fuscidulum* and the bearing of these results on the relationship of the three species will be examined.

Saccardo (1883, p. 141) suggested *Phoma ulmicola* Berk. (in Hook. *J. Bot. Kew* (1853), XL, pl. 3, fig. 3) as the pycnidial condition of *Thyridaria rubro-notata*. Grove (1935, p. 140) has examined Berkeley's specimen and states that the species is an *Aposphaeria* and probably a juvenile condition of *A. agminalis* Sacc. which I consider to belong to *Melanomma Pulvis-pyrius*. The brothers Tulasne described the imperfect stage of *Thyridaria rubro-notata* in detail (1863, p. 243).*

They compared the pycnidia and perithecia of their own collections on *Aesculus Hippocastanum* and *Ribes* with collections received from Berkeley on *Ulmus*. They state that: "The pycnidia, which seem to constitute *Phoma ulmigenum* Berk. . . . are usually found solid; . . . their thin wall is divided from the contents, which have the same colour, viz. cinereous—or greenish-fuliginous, by a white continuous and very narrow zone, made up of very crowded sterigmata. . . ." The conidia are described as: "Straight, continuous, muticous, smooth, pale fuliginous (at least when seen separately), about 6·5 μ long, and half as wide." Further, they say: "*Melogramma rubro-notata* Berk. & Br. and *Phoma ulmigenum* or *ulmigena* Berk. are also cited in Berkeley's *Outlines of British Mycology*, p. 314, no. 19, and p. 391, no. 1, but without any description." Berkeley's species was *P. ulmicola*—the specific epithet applied by the brothers Tulasne is due to a slip of the pen.

Petrak and Sydow (1927, p. 449) refer the pycnidial stage to *Cytoplea juglandis* (Schum.) Petr. and give a list of synonyms, some of which will be discussed below, followed by a very full description of the pycnidial fungus. The genus *Cytoplea* Bizz. & Sacc. (*Flor. Venet. Critt.* 1885, p. 401) was erected to include species having multilocellate, superficial pycnidia containing ovoid-oblong, olivaceous-fuliginous conidia arising in series from well-defined sporophores and at first attached together in chains but soon separating. (The "paraphyses" mentioned by the authors (*loc. cit.*) are, perhaps, simply long sporophores—vide supra, p. 129.)

The pycnidia occurring upon *Ulmus* and *Acer* (vide Table IV) may be briefly described as follows: Immersed within the cortex or superficial on decorticated wood, clustered in groups of 2–4 individuals or singly, rugose, black, 500–1000 μ in diameter (Pl. VI, fig. 3), closely surrounded at the base by a mass of mycelium consisting of coarse, brownish hyphae, covered by bright red to brick-red hyphae when young but dusted, when mature, round the wide ostiolum, by a reddish farina composed of the collapsed segments of the reddish mycelial byssus. Wall of carbonaceous texture, enclosing a pseudolocellate cavity lined by a conspicuous zone of sporophores (Text-fig. 2 F). Conidia, discharged in sticky, greenish black, glistening masses,

* The number given refers to the page in the original edition, not the English translation from which the following description is transcribed.

globose or ovate-cylindrical, rounded at each end, at first hyaline and uni- or biguttulate, later becoming yellowish and finally pallid-olivaceous, 5–8 × 2·5–4 μ (mostly 5–7 × 2·5–3·5 μ, (Text-fig. 2 G, H, K). Sporophores cylindrical or somewhat flask-shaped, erect, 10–15 × 2–5 μ, bearing short chains of hyaline or yellowish spores. This description also applies to pycnidia in culture on agar or on wood either from ascospores or conidia with the exception that, in culture, the pycnidia are usually solitary and entirely surrounded by a bright orange, reddish orange or bright vermilion byssus. On agar they are clearly differentiated from the white mycelium which is streaked with strands of red or orange hyphae. On wood any superficial mycelium present is rather brownish and consists of a very thin, closely applied mat of hyphae.

The sporophores are typical phialides (Text-fig. 2 G, H) resembling in shape those in the pycnidia of *Melanomma Pulvis-pyrius* and *M. fuscidulum*. The basipetal sequence of the phialospores is clearly indicated in the chain of conidia attached to the phialide, since the youngest spore is hyaline and the oldest yellowish or slightly olivaceous.

Isolations from the collection on *Acer* produced mycelia and pycnidia indistinguishable from those from *Ulmus*. The perfect stage on each host is precisely similar and there can be no doubt that they represent collections of the same species on two different hosts.

Petrak and Sydow (1927) when discussing the synonymy of *Cytoplea Juglandis* question whether *Coniothyrium incrustans* Sacc. (in *Atti. Soc. Venet. Trent. Sc. nat.* IV (1875), 114) is a valid synonym. *C. incrustans* is, according to Saccardo, the pycnidial stage of *Thyridaria incrustans* Sacc. (*Myc. Ven.* II, 170) which Petrak and Sydow suggest may not be specifically distinct from *T. rubro-notata*. Saccardo first described and figured *T. incrustans* in *Mycologiae Venetae specimen* (1873), 118, as *Cucurbitaria Broussonetiae* Sacc. and stated that it possessed two imperfect stages—both pycnidial—of which the first (*Coniothyrium incrustans*) had ovoid, fuscous conidia 3–4 × 5 μ, while the second (*Diplodia incrustans*) had bicellular fuscous conidia, 15 × 10 μ. In the specimen in the Herbarium of the British Museum (*Myc. Ven.* no. 170) *Diplodia* spores are found free on the surface of some of the perithecia; they have never been observed in situ in pycnidia. I have not observed the spores referred to *Coniothyrium incrustans* which Petrak and Sydow suggest should be transferred to *Cytoplea Juglandis*. The ascophorous stage, while similar in general characters to *Thyridaria rubro-notata*, is definitely not that species. The asci and ascospores are distinctly larger than those of *T. rubro-notata*, being respectively 110–148 × 10–16 μ and 22–27 × 8–10 μ and the ascospores are arranged in a distichous manner. If *Coniothyrium incrustans* is a *Cytoplea* and is actually a stage in the life cycle of *Thyridaria incrustans* the synonymy *suggested* by Petrak and Sydow is incorrect.

These authors also give *Phoma ulmicola* Berk. and *P. ulmigenum* Tul. as synonyms of *Cytoplea Juglandis*. They have not examined the type specimen of the former (vide supra, p. 129) and the latter name has been incorrectly applied by Tulasne (vide supra, p. 134).

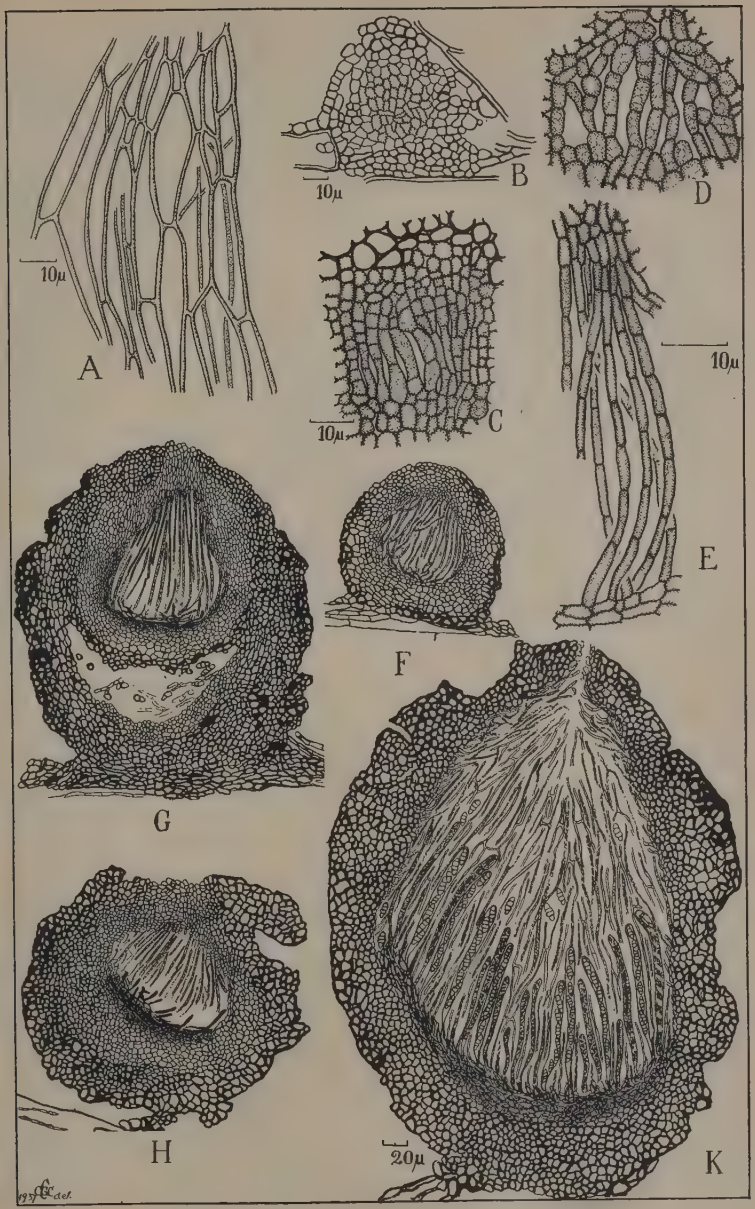
The following facts emerge from this study of *Thyridaria rubro-notata*. *T. incrustans* Sacc., the type species of the genus, is quite distinct from *T. rubro-notata* which has been examined on, and isolated from, *Ulmus* and *Acer*. The perfect and imperfect states of this species on each host are strictly comparable and isolations yield exactly similar cultures. The imperfect stage of this species has simple sporophores (phialides) similar in all respects to those of the *Aposphaeria* stages of *Melanomma Pulvis-pyrius* and *M. fuscidulum* and develops serial conidia (phialospores) differing only in size and colour from those of the other species.

(*b*) *The ascophorous stage*

The perfect state of *Melanomma Pulvis-pyrius* and *Thyridaria rubro-notata* have been developed on fresh branches of several hosts inoculated with active mycelium from agar cultures. Mature ascocarps were obtained only after the inoculated branches had been placed out of doors (usually after a total incubation period of from six to nine months). Ascocarps of the former species are easily obtained and a full account of their development is given; those of the latter only with difficulty and unfortunately extremely few early stages of development have been available for study. No ascocarps of *M. fuscidulum* have as yet been obtained on inoculated tissues and the results reported below are based on examination of collected material.

(1) *Melanomma Pulvis-pyrius*.

The ascocarp commences as a mass of pseudoparenchyma, the outermost cells having brown, thick walls (Text-fig. 3 B). The long axis of the central cells lies parallel to the long axis of the ascocarp (Text-fig. 3 C). During growth the central cells become densely stained and separate into strands which remain attached to the outer cells at the apex and base of the ascocarp (Text-fig. 3 D) to form what may be termed *trabeculae*. As the ascocarp enlarges, the trabeculae keep pace by growth and division of their constituent cells (Text-fig. 3 E and F). These trabeculae must be visualized as branched anastomizing filaments forming a network in the centre of the ascocarp. So far no asci are present but very soon they commence to develop in the base of the ascocarp (Text-fig. 3 G). The details of the development of the asci have not been studied. They are confined to a basal plate (Text-fig. 3 H). The ascocarp is still completely closed, but with the elongation of the asci, which grow upwards amongst the now widely separated trabeculae, indications of a break in the con-



Text-fig. 3. *Melanomma Pulvis-pyrius* (Pers.) Fuckel.

A. Trabecular pseudoparaphyses excised from a ripe perithecium.
B–K. Stages in the development of the perithecium, for further details see text.
(The scale of the drawings D and E is similar, that of F–K is given under K.)

tinuity of the apical region may be observed. In the mature ascocarp the asci form a concave layer within the base of the ascocarp and project upwards amongst the trabeculae (Text-fig. 3 K). Although many of the trabeculae are severed in thin sections, several can still be traced from the base of the ascocarp to their junction with the tissues of the apical area. They persist even in the oldest ascocarp (Text-fig. 3 A). The asci ripen in series so that even in mature ascocarps there are many in which the ascospores are yet undifferentiated.

Such a sequence of stages indicates that the ascocarp is stromatic, and that its development is typically dothideaceous. The asci appear only after the stroma has reached a considerable degree of differentiation. True paraphyses and periphyses are not formed. The stromatic character of the ascocarp is of fundamental importance. In the first study of this series (1935, p. 261) I said: "It is not intended to consider here the validity of Pyrenomycetes as a specialized class within the Ascomycetes; in this series of papers the word is used in the sense employed by Winter." According to this writer (1884, p. 220) the Pyrenomycetes include a very heterogeneous collection of forms and *Melanomma* is placed in the family Melanommeae of the Sphaeriaceae along with *Rosellina*, *Bombardia*, *Melanopsamma*, and *Bertia*. Von Höhnel, and Theissen and Sydow have studied numerous species belonging to this class and have advanced the opinion that many species described as perithecial are stromatic (unilocular stromata) and have, therefore, no place in the Sphaeriales (Sphaeriaceae of Winter). Miller (1928*a*, p. 188) has reviewed their findings and pointed out that while they recognize the stromatic types that have their asci contained within a single loculus, they yet attempt to connect these forms with those having true perithecia by means of intermediate stages in which the thickness of the stroma is progressively reduced. Species possessing unilocular stromata must be related to the Dothideales. To Miller the presence of a true perithecial wall is a fundamental criterion of a true perithecium. I believe that the recognition of this as a basic criterion will definitely advance the study of the phylogenetic classification of the Sphaeriales and in order to leave no doubt as to the meaning given by Miller to the term "perithecial wall" and as to the implications involved in the acceptance of his views I give a summary of his statements (1928*a*, p. 194). He considers that the occurrence of a perithecial wall is correlated with certain characters of the perithecial centrum. Where a true wall is lacking the centrum is pseudoparenchymatous, paraphyses and periphyses are not present and the ascocarp opens in a lysigenous manner. Where there is a true wall the centrum is not pseudoparenchymatous, paraphyses and periphyses occur and the ostiolum develops schizogenously. The wall is different in structure and origin

from the stromatic tissue. Miller defines it as "The specialized tissue, which arises from the archicarp, and from the beginning encloses the ascigerous centrum. None of the cells of the wall are derived from those of the stroma other than those of the archicarp."

The development of the ascocarp of *Melanomma Pulvis-pyrius* commences with a mass of pseudoparenchymatous tissue. True paraphyses arising from the hymenial layer are not present. In reviewing the development of paraphyses in stromatic types (Pseudosphaeriales and Dothideales) Petrak (1924, p. 67) groups the genera into three classes: (1) having no paraphyses (e.g. *Mycosphaerella* and *Sphaerulina*); (2) having paraphyses formed from persistent parts of the pseudoparenchyma (e.g. *Pleospora* spp. and *Leptosphaeria* spp.); (3) having persistent, branched paraphyses attached to the apical tissues of the fructifications (e.g. *Melanomma* spp., *Leptosphaeria* spp. and very many others including dothideaceous fungi). When dealing with types having a true perithecium he denies the presence of true paraphyses and terms the structures arising from the hymenium, pseudoparaphyses, which he defines as having free apices in contrast to the true paraphyses which are attached at the apices. In his sense "paraphyses" are only persistent portions of stromatic tissue. This is not the original conception of the term. Where true paraphyses are present in perithecial or apothecial fructifications they *grow from* the hymenial layer. Miller (1928*a*, pp. 199–201) describes the development of and mature structure in the ascocarps of *Chaetosphaeria phaeostroma* (Mont.) Sacc., *Dibotryon morbosum* (Schw.) Th. & Syd. and *Leptosphaeria Doliolum* (Pers.) Wint. which correspond to Petrak's second and third types of stromatic forms. *Chaetosphaeria phaeostroma* is stated to be characteristic of the Pseudosphaeriales of Theissen and Sydow (1918). At first it is a pseudoparenchymatous stroma. In the lower part an archicarp later appears from which the ascogenous hyphae and asci develop. The latter penetrate the pseudoparenchyma whose cell walls become progressively thinner and finally dissolve. Miller compares this tissue to the tapetal layers of anthers in flowering plants. The apical opening of the stroma is lysigenous in origin but the final breaking of the tissues is due to the expansion of the hymenial layer. This opening is not a true ostiolum as the passage is lined by broken cell elements and not by periphyses which "are outgrowths of basal cells in the neck wall and have free ends" (Miller, 1928*a*, p. 197). Miller states that the development in the other two species is similar.

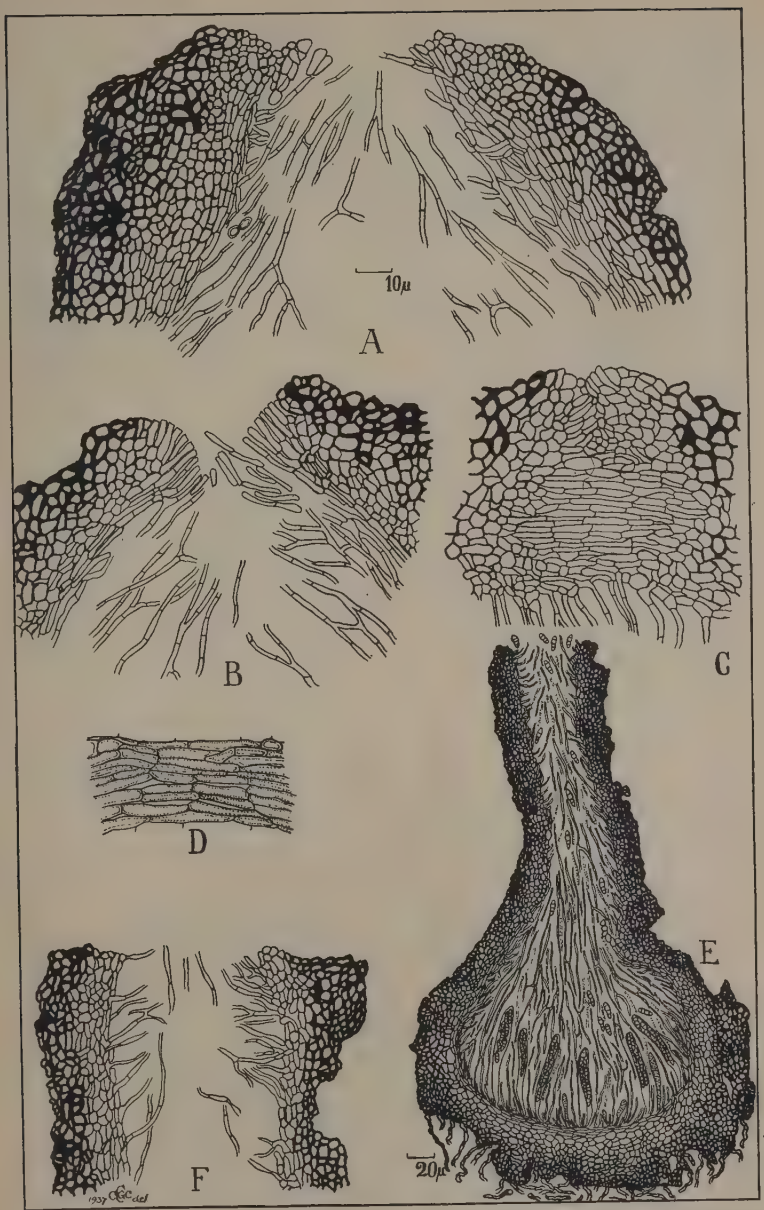
The ascocarp of *Melanomma Pulvis-pyrius* shows only a certain degree of similarity with *Chaetosphaeria phaeostroma*. It is stromatic but the tissue into which the asci grow is persistent and accommodates the developing hymenium by continual growth of its trabecular elements. I can find no evidence of dissolution of the tissues nor are any ragged

lateral walls present on the trabeculae. These are always one cell in breadth. They form a network attached to the inner wall of the stromatic cavity; they are persistent. The pore is developed by a process involving partial change of the wall material and a separation of the tissue elements. At any point on the apical part of the stroma an area of cells may undergo the following changes. The cell walls gradually lose their brown colour (Text-fig. 4 C) and appear to expand in a tangential direction without actual division to give a laminated appearance to the tissue. The brown colouring matter is absent for a varying distance amongst the surrounding cells. The trabeculae are still attached to the inner side of this discoloured tissue (Text-fig. 4 C). The central cells of the thin-walled area separate slightly from one another (Text-fig. 4 D). Finally the laminated thin-walled cells separate along a longitudinal line. The cells do not appear to be torn across but merely to separate between their several longitudinal walls (Text-fig. 4 B). The separation of these cells releases the trabeculae which project into the gap so formed (Text-fig. 4 A). The opening of the stroma does not occur at any particular point nor is its appearance governed by any pre-existing conformation of the surface (e.g. a raised papilla). In fact, as often as not, where a papilla is present the opening may be on a much lower level. When the opening is sulcate the thin-walled area is large and suture lines radiate from a common centre.

(2) *Melanomma fuscidulum.*

Young stages of the ascocarp of this species were not discovered in sufficient quantity to allow of a detailed study. This was all the more disappointing as the formation of the opening in the neck requires careful study. From observation of the material available, however, it is evident that the ascocarp is stromatic in origin and development. The asci grow upwards into a mass of trabecular filaments similar to those present in *M. Pulvis-pyrius* (Text-fig. 4 E). The neck is not traversed by a true ostiolum ("the canal passing through the papilla, or neck of the perithecium, and terminating in a pore. It is lined with minute periphyses . . ." (Miller, 1928*a*, p. 197)). The cavity within the neck is lined by torn cells and by filaments separated from the hyaline cells of the stromatic wall, and, prior to active spore discharge, by a mass of trabecular filaments (Text-fig. 4 F).

Where the stromata occur as superficial structures on the wood (less often upon the periderm) of the host, several of them are surrounded by a network of coarse brown to brownish green hyphae which may frequently develop into a mound of plectenchymatous tissue lying below groups of unilocular stromata (Text-fig. 5 B). The presence of this tissue raises the question of the application of the term stroma. The ascocarps of this species might well be considered



Text-fig. 4. A–D. Stages in the formation of the pore in the perithecium of *Melanomma Pulvis-pyrius*.
E. Median section through a mature perithecium of *Melanomma fuscidulum*.
F. Median section through the apex of the neck of such a perithecium.
(With the exception of E, all drawings are to the same scale, given under A.)

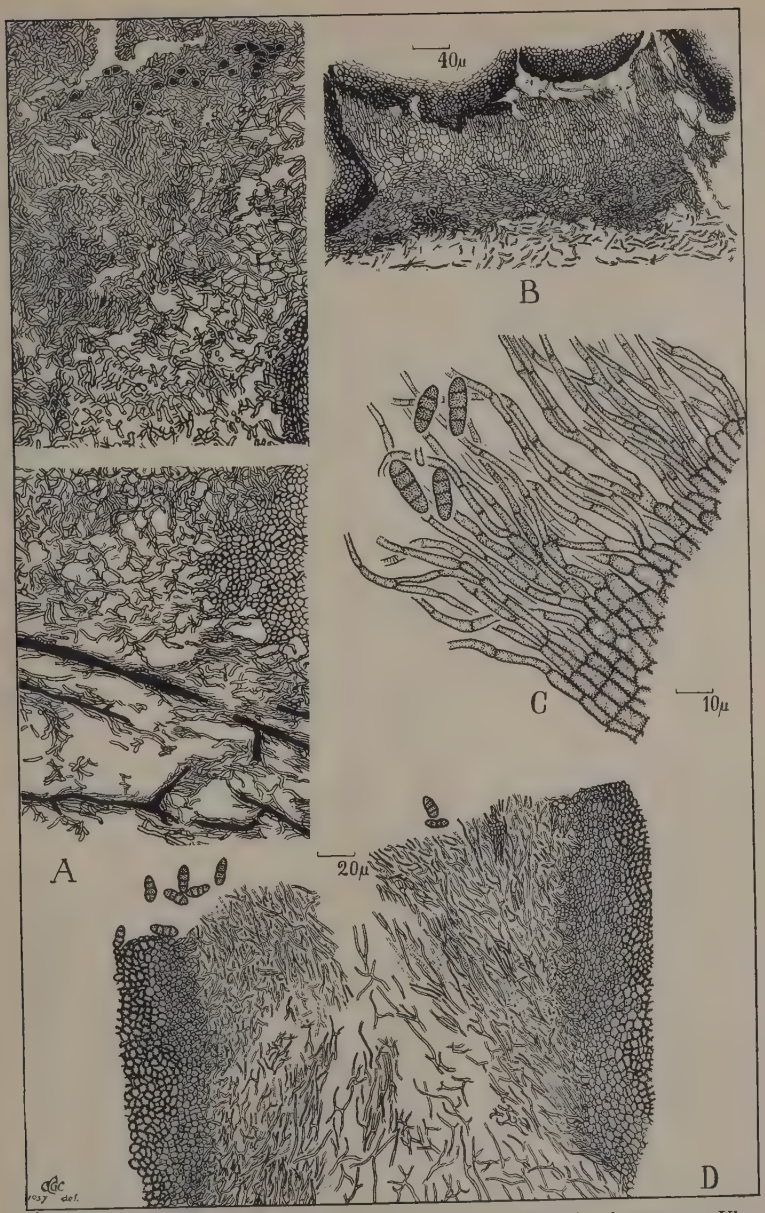
to be perithecia developing on the surface of a stroma were it not that they have a dothideaceous type of development. This mycelial mat is not so obvious when the stromata are immersed in hard or decayed wood, but it still exists as a mesh of coarse brown hyphae spreading from one ascocarp to another and forming a thin, almost plectenchymatous skin on the surface of the wood. The pycnidia are formed beneath it and the ascophorous stromata grow up through it. If the periderm is carefully removed from about immersed ascocarps these are seen to be surrounded by masses of mycelium connected with one another by strands of brownish hyphae passing along the wood surface. This aggregation of mycelium and the more compact plectenchymatous cushions may be considered subicular; they represent local aggregations of the vegetative hyphae and are probably to be explained by the localized type of growth of the mycelium.

Melanomma fuscidulum is considered to show a development exactly comparable with *M. Pulvis-pyrius*. The ascocarps are stromatic in structure, exhibit the dothideaceous type of development and are associated with a restricted and often pustular mycelium. The neck is not comparable with the neck of a true perithecium; its cavity is traversed in the youngest condition observed by a network of trabecular filaments and is never lined with periphyses. The aggregation of stromata in discrete groups is to be correlated with the slowly growing and more restricted spread of the mycelium as compared with that of *M. Pulvis-pyrius*.

(3) *Thyridaria rubro-notata.*

Very few early stages of the ascocarp have been observed and the following details refer particularly to the more or less mature structure. The relationship of the pycnidia and ascocarps to the mycelium is briefly discussed in relation to the taxonomy of the species.

In culture the pycnidia and ascocarps are formed both within the cortex and on the surface of decorticated wood. They are invested by a loose mass of reddish yellow or deep red hyphae which are intertwined to form a pustule. In nature the pycnidia may occur with the ascocarps or separately but they are always invested by similar networks of mycelium. Saccardo (1883, p. 3) places *Thyridaria* with *Aglaospora* and *Pseudovalsa*, and beside *Kalmusia* and *Melogramma* in the composite Phaeophragmiae. He distinguishes the first three genera by what he terms their valseoid stromata, *Kalmusia* by the effuse, eutypoid, stroma and *Melogramma* by the emergent, pulvinate stroma. When giving the generic characteristics he (1883, p. 140) describes the perithecia as occurring in almost valseoid acervuli immersed in the cortex and having the surface of the stroma joined to the subcortical tissue, the disc of the stroma being mealy, yellow or red. Sections of the perithecial pustule show that each ascocarp



Text-fig. 5. A. Longitudinal section through a pustule of *Thyridaria rubro-notata* on *Ulmus*. The disintegrated tissues of the host cortex are shown in black at the base of the drawing.

B. Longitudinal section through the plectenchymatous mass of mycelium below the perithecia of *Melanomma fuscidulum* within the cortex of *Fagus*.

C. Illustrating the branching of the pseudoparaphyses of *Thyridaria rubro-notata*.

D. Median section through the neck of a perithecium of *T. rubro-notata*.

(The drawings A and B are to the same scale; that of C and D is given on each drawing.)

is limited by a layer of very clearly defined dark pseudoparenchymatous tissue from the mycelial vestment. The appearance of the longitudinal section is that of ascocarps immersed in a very loose stroma (Text-fig. 5 A). Yet within each ascocarp exist similar conditions to those obtaining in *Melanomma Pulvis-pyrius*. The asci arise from a slightly concave hymenium and grow upwards into a plexus of trabecular filaments. The neck is only a little less in diameter than the venter of the ascocarp and scarcely tapers. The opening is apparently formed by the separation of the hyaline tissue which at first completely fills the neck. At maturity the inner face of the passage is lined with partly separated filaments of cells and trabecular elements arising from the base of the stroma (Text-fig. 5 D). Periphyses such as occur in the perithecia of true Sphaeriales are never present, although under low powers of the microscope the separated filaments give the appearance of a zone of periphyses.

It is my opinion that *Thyridaria rubro-notata* possesses pycnidia and perithecia (which develop as dothideaceous-like stromata) embedded in pustular aggregations of the widespread mycelium. While each pustule may be regarded as a stroma this type of structure must be clearly segregated from the stromata occurring in the Allantosphaeriaceae or the Xylariaceae which contain true perithecia.

IV. Discussion

(1) *The imperfect stage*

It has been shown that the three species examined have each a pycnidial stage producing small amerosporous conidia extruded in slimy masses from the conceptacles. The conidia arise in basipetal succession from the apical growing point of a unicellular filament or phialide. They are therefore serial meristem spores (Mason, 1933, p. 9). The phialides are of similar structure in all the species. In the species of *Melanomma* the conidia are hyaline but of different size and shape, while in *Thyridaria rubro-notata* they become coloured when mature. This similarity of the phialides and phialospores is not without significance when considered along with the structure and development of the ascocarp in each species and the shape of the ascospores. Relationship must be based on the agreement of a number of separate criteria—one of which must be the structure and development of the accessory spore form. In the future it is probable that greater attention will have to be paid to the origin of the conidia and much less to such a variable character as colour if a rational understanding of the relationship of imperfect stages belonging to similar ascophorous states is to be attained. I consider that the important features disclosed by a study of the conidial forms of the three species

examined are (1) that the conidia invariably arise in series from the apices of phialides; (2) that the phialides are sessile; (3) that the conidia exude in a slimy mass from pycnidia. The colour of the conidia and the actual structure of the pycnidial wall are very subsidiary characters; it is the character of the sporing hymenium and what is taking place during the development of the conidia that requires full attention. The species of *Aposphaeria* and *Cytoplea* have been erected upon the relationship of the pycnidia to their substratum, the shape and texture of the pycnidial wall and the colour and shape of the conidia. Such characters are important from the point of view of taxonomy, but for any phylogenetic studies the detailed development of the hymenium should rank as the primary criterion of relationship. From this point of view the imperfect stages described here must be placed in close proximity—a conclusion confirmed by the examination of the ascophorous stages.

(2) *The perfect stage*

In *Melanomma Pulvis-pyrius* the ascocarp is a stroma and the single locule containing the asci is the result of a growth process during which trabeculae are formed. These represent the highest development of what Petrak (1924) called "paraphyses" and are to be contrasted with the stromatal remnants produced by a process of dissolution within the centrum of the stroma of certain species of *Leptosphaeria* and *Chaetosphaeria*.

The exact definition of the term stroma as applied to Pyrenomycetes is bound to remain a difficulty until it is realized that the stromata of the Pseudosphaeriales—Dothideales section is a thing apart from the stroma in the Sphaeriales. Miller (1928*a*, p. 191) defines stromata as: "Fungous bodies which are formed of coalesced hyphae, which do not arise as a result of a sexual stimulus." He applies this definition to stromata of members of the Pseudosphaeriales. I think this is impossible, as in such species as have been examined the stroma increases in size by the active growth and subsequent division of a few initial cells. There is no continued, progressive coalescence of originally free hyphae such as occurs in either *Diatrype*, *Diatrypella*, *Anthostoma* or *Hypoxylon*, although even here the intertwined hyphae increase in quantity by active growth and division. De Bary (1887, pp. 229, 247) realized this difference with regard to pycnidia and termed those *meristogenetic* which were formed by growth and division of a few initial cells and those *symphogenetic* which were formed mainly by the coalescence of hyphae. He also realized that intermediate conditions existed in which part of the pycnidium was meristogenetic and part symphogenetic. Vuillemin (1912, p. 144) applied the terms *merenchyma* and *synenchyma* to fungal tissues produced,

respectively, by division and by fusion. The differentiation of these two modes of tissue production appears to me to be particularly appropriate in the differentiation of the ascocarps of the Pseudosphaeriales from those of the true Sphaeriales. The latter have symphogenetic stromata consisting in the main of synenchyma in which the perithecia arise from definite archicarps that produce the perithecial wall, ascogenous hyphae and asci. The former have meristogenetic stromata composed of merenchyma within which an archicarp produces a hymenium of ascogenous hyphae from which asci grow upwards into the pseudoparenchymatous or trabecular centrum of the stroma. If such terminology were adopted it would allow for the condition which is apparently foreshadowed in *Melanomma fuscidulum* and *Thyridaria rubro-notata* where the *meristogenetic* stroma containing asci is seated upon or enclosed in a poorly developed *symphogenetic*, purely vegetative, stroma produced by a local coalescence of the mycelium. This condition is seen in a more advanced state in species of *Cucurbitaria* where the ascocarp (which is of dothideaceous structure) arises from the surface of such a stroma. Only a full investigation of representative species can prove or disprove the correctness of this thesis, but I submit it as a possible means of solving a problem which has so far been overlooked. The stroma of species of the Allantosphaeriaceae and of Xylariaceae is not analogous with the ascocarpic stroma of species of the Pseudosphaeriales and the two structures must not be compared.

The facts recorded above indicate that the species of *Melanomma* investigated ought to be placed in the Pseudosphaeriales. They are not related to *Rosellinia* as suggested by Winter (1884). Species of this genus have been shown by Miller (1928*b*, p. 326) to belong to the Xylariaceae and are true Sphaeriales. It is probable that species of *Bertia* and *Melanopsamma* will be found to have a similar development to that of *Melanomma* and to belong to the Pseudosphaeriales. If a complete review of the Pyrenomycetes is ever written, in which numerous criteria are used as a basis of generic separation, I am certain that species of *Thyridaria* will then find a place close to the species of *Melanomma* discussed here. They are not congeneric but they bear a relationship in structure of both perfect and imperfect stages which is too definite to be disregarded.

The species described here must be separated from certain species now placed in the genus *Leptosphaeria*, which have also triseptate phaeophragmospores. The former have perithecia with a persistent, trabecular centrum into which the asci grow; of the latter, *Leptosphaeria Doliolum* (Pers.) Wint. is stated by Miller (1928*a*, p. 208) to have a pseudoparenchymatous centrum the cells of which "separate into thin strands which hang down between the asci at maturity". In the three species already described (vide supra, p. 120) the very

characteristic development of the ascospore which results in a spindle-shaped, four-celled spore with the two anterior cells of a greater width than the two posterior cells is to be contrasted with that of the *Leptosphaeria* ascospore. Here the equatorial septum divides the spore into two equally wide cells which remain so after the development of the final septum in each cell. The conidia of the species now described are slimy meristem phialospores, hyaline in *Melanomma* and tinted in *Thyridaria*. The conidia reported as associated with *Leptosphaeria Doliolum* are hyaline, *Phoma*-like spores apparently arising directly from the cells lining the pycnidium. It is highly probable that they fall into the group described by Mason (1937, p. 91) as slimy radulospores. The conidia of *L. Coniothyrium* are tinted, slimy radulospores.

I believe that species of *Melanomma*, based on *M. Pulvis-pyrius* as the type species, and species of *Thyridaria* (provided that *T. incrustans*, the type species, is found to possess developmental characters similar to those of *T. rubro-notata*) constitute a group within the Pyrenomycetes which is characterized by the dothideaceous-like development of the ascocarp as a whole and the persistence of its central tissues, the peculiarly shaped, triseptate ascospores and the slimy, meristem phialospores. This group lies in relation to, but is more advanced than, a group exemplified by the species of *Leptosphaeria* with triseptate ascospores which is characterized by an equally dothideaceous-like ascocarp, by ascospores of even width and by a less advanced conidial apparatus represented by the slimy radulospores (cf. Mason, 1937, p. 89—last sentence). The former group contains species with solitary perithecia and species, like *Thyridaria rubro-notata*, with perithecia immersed in a stroma but because of the development of these perithecia such stromatic forms must not be placed in relation to stromatic Sphaeriales having true perithecia.

V. Summary

Melanomma Nitschke emend.

1. Perithecia gregaria, interdum sparsa, initio immersa at tandem semper superficialia, matrici plus v. minus evoluto subiculo adnata, sphaerica v. subglobosa, apice rotundata, papillata aut conspicue rostrata, carbonacea, laevia aut rugosa, pseudoparaphysibus (trabeculis) persistentibus, ramosis anastomosantibus, septatis, hyalinis farcta. Asci cylindrici v. clavato-cylindrici, octospori. Sporidia monosticha v. disticha, fusoidea, nonnunquam curvula, saepius triseptata, cellulis anterioribus quam posteriores latioribus, luteola vel atrobrunnea.

2. Pycnidia forma digestioneque peritheciis simillima, at minora nec unquam conspicue rostrata. Conidia ellipsoidea v. oblonga,

utrinque rotundata, hyalina, mucosa, meristematico-phialospora, conidiophoris bene evolutis suffulta.

Sp. typ. *M. Pulvis-pyrius* (Pers.) Fuckel.

1. *Perithecia* gregarious, occasionally scattered, initially immersed but finally always superficial on the host matrix or on a more or less well-developed subiculum, spherical or irregularly globose, apex dome-shaped, papillate or conspicuously beaked, carbonaceous, smooth or rugose; interior filled by persistent, branched and anastomosing, septate, hyaline pseudoparaphyses (trabeculae). Asci cylindrical or clavate-cylindrical, eight-spored. Spores monostichous or distichous, spindle-shaped, often slightly curved, usually triseptate, width of the two anterior cells greater than that of the two posterior cells, yellowish or dark brown.

2. *Pycnidia* similar in shape and distribution to the perithecia but smaller and never conspicuously beaked. Conidia ellipsoid or oblong, rounded at each end, hyaline, produced as slimy, meristem phialospores from well-defined conidiophores.

Type species: *Melanomma Pulvis-pyrius* (Pers.) Fuckel.

(*a*) *Ascospores monostichous*. Perithecia spherical or globose, apex rounded or papillate. Ascospores yellowish, 11·5–18 × 4 μ (14–16 × 5 μ). Phialospores 2–3·5 × 1·5–2·5 μ (*Aposphaeria agminalis* Sacc.) *M. Pulvis-pyrius*.

(*b*) *Ascospores distichous*. Perithecia flask-shaped, neck more or less elongate. Ascospores dark brown, 12–16 × 3–4·5 μ (14 × 5). Phialospores 3·5–5 × 2·5–3 μ (4 × 3). (*Aposphaeria fuscidula* Sacc.) *M. fuscidulum*.

Thyridaria Sacc. emend.

1. Perithecia in pustulas solitarias stipata, rarissime solitaria, mycelio effuso immersa, disco saepissime farina rubra v. rubroluteola consperso, late ovoidea, rostro praedita, pseudoparaphysibus (trabeculis) persistentibus ramosis anastomosantibusque, septatis, hyalinis, farcta. Asci cylindrici v. subclavati, octospori. Sporidia monosticha v. disticha, fusoidea, rarissime curvata, saepissime triseptata, cellulis anterioribus nonnihil quam posteriores latioribus, atrobrunnea, saepe ferme opaca.

2. Pycnidia cum peritheciis in stromate communi associata, aut solitaria stromate vix evoluto. Conidia ovato-cylindrica v. subglobosa, primo hyalina, dein pallide olivacea, mucosa, meristematico-phialospora conidiophoris bene evolutis suffulta.

Sp. typ. *T. incrustans* Sacc.

1. *Perithecia* grouped in isolated pustules, seldom solitary, immersed in a loose, purely mycelial stroma, disc frequently dusted with a red

or reddish yellow farina, broadly flask-shaped, containing persistent, branched and anastomosing, septate, hyaline pseudoparaphyses (trabeculae). Asci cylindrical or slightly clavate, eight-spored. Spores monostichous or distichous, spindle-shaped, seldom curved, commonly triseptate, width of the two anterior cells slightly greater than that of the two posterior cells, dark brown to almost opaque.

2. *Pycnidia* associated with the perithecia in a common stroma or singly and then surrounded by a poorly developed stroma. Conidia ovate-cylindrical or globose, at first hyaline, later pallid-olivaceous, formed as slimy, meristem phialospores from clearly defined sporophores.

Type species. *T. incrustans* Sacc.

(*a*) *Ascospores monostichous.* Ascospores dark brown, $15–18 \times 5–6\,\mu$ ($16 \times 5–6$). Phialospores $5–8 \times 2{\cdot}5–4\,\mu$ ($5–7 \times 2{\cdot}5–3{\cdot}5\,\mu$.). (*Cytoplea juglandis* (Schum.) Petr.) *T. rubro-notata.*

(*b*) *Ascospores distichous.* Ascospores brown to dark brown, $22–27 \times 8–10\,\mu$. Phialospores not seen. *T. incrustans.*

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REFERENCES

De Bary, A. (1887). *The Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria.* Eng. Trans.

Brefeld, O. (1891). *Untersuchungen aus dem Gesammtgebiete der Mykologie*, x, Ascomyceten, II.

Chesters, Chas. G. C. (1935). "Studies on British Pyrenomycetes. I." *Trans. Brit. mycol. Soc.* xix, 261–79.

Diedicke, H. (1915). *Kryptogamenflora der Mark Brandenburg*, ix.

Farries, E. H. M. & Bell, A. F. (1930). "On the metabolism of *Nematospora Gossypii* and related fungi, with special references to the source of nitrogen." *Ann. Bot., Lond.*, xliv, 423–455.

Grove, W. B. (1935). *British Stem- and Leaf-Fungi (Coelomycetes)*, I.

Hawker, Lilian, E. (1936). "The effect of certain accessory growth substances on the sporulation of *Melanospora destruens* and of some other fungi." *Ann. Bot., Lond.*, l, 699–718.

Mason, E. W. (1933). *Annotated Account of Fungi Received at the Imperial Mycological Institute*, List II, fasc. 2.

—— (1937). *Annotated Account of Fungi Received at the Imperial Mycological Institute*, List II, fasc. 3.

Miller, J. H. (1928*a*). "Biologic Studies in the Sphaeriales. I." *Mycologia*, xx, 187–213.

—— (1928*b*). "Biologic studies in the Sphaeriales. II." *Mycologia*, xx, 305–39.

Petrak, F. (1924). "Mykologische Notizen VII (301–400)." *Ann. mycol.* xx, 1–182.
Petrak, R. & Sydow, H. (1927). "Die Gattungen der Pyrenomyceten Sphaeropsideen und Melanconieen." *Repert. nov. Spec. Regn. Veg.* xlii, Beih. 3.
Saccardo, P. A. (1878*a*). "Fungi Veneti Novi vel Critici. Ser. VII." *Michelia*, i, 133–221.
—— (1878*b*). "Fungi Italici autographice delineati, Fasc. v–viii, tab. 161–320. Commentarium." *Michelia*, i, 326–50.
—— (1878*c*). "Fungi Veneti Novi vel Critici. Ser. III. (ex *Hedwigia*, xiv (1875))." *Michelia*, i, 446–52.
—— (1881). "Fungi Veneti Novi vel Critici. Ser. XII." *Michelia*, ii, 241–301.
—— (1883). *Sylloge Fungorum*, ii.
—— (1884). *Sylloge Fungorum*, iii.
Theissen, F. & Sydow, H. (1918). "Vortenwurfe zu den Pseudosphaeriales." *Ann. mycol.* xvi, 1–34.
Tulasne, L. R. & C. (1863). *Selecta Fungorum Carpologia*, ii.
Vuillemin, P. (1912). *Les Champignons—Essai de Classification.*
Winter, G. (1884). In *Rabenh. Krypt. Fl. I*, Abt. ii.

EXPLANATION OF PLATES VI AND VII

Plate VI

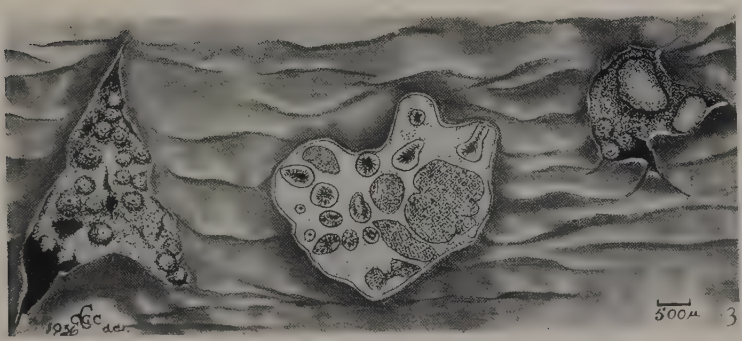
Fig. 1. A group of perithecia of *Melanomma Pulvis-pyrius* (Pers.) Fuckel on *Corylus*.
Fig. 2. A group of perithecia of *Melanomma fuscidulum* Sacc. on *Fagus*; the periderm has been removed to show the perithecial venters and the mycelial subiculum.
Fig. 3. Pustules of *Thyridaria rubro-notata* (B. & Br.) Sacc. on *Ulmus*. That on the left contains only perithecia; that on the right both perithecia and pycnidia; that in the centre has been cut transversely to show the perithecia and pycnidia (densely stippled) embedded in the stromatic tissue.

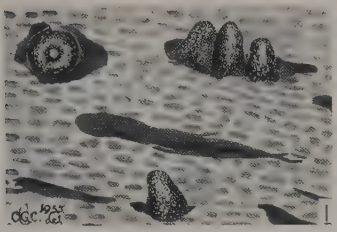
Plate VII

Fig. 1. Perithecia of *Melanomma fuscidulum* from Saccardo's *Myc. Ven. Spec.* 159.
Fig. 2. A culture of *Melanomma Pulvis-pyrius* (no. 1225) on malt agar showing very abundant pycnidia.
Fig. 3. Pycnidia of *Melanomma Pulvis-pyrius* on a lentil-extract agar culture which was derived from a single conidium from pycnidia collected on *Ulmus* (no. 198 A).
Fig. 4. A drawing of the pycnidia on *Ulmus* (no. 198 A).
Fig. 5. Pycnidia similar to those of Fig. 3 but growing on a single ascospore culture from the collection on *Ulmus* (no. 198).
Fig. 6. Pycnidia and perithecia of *Melanomma fuscidulum* on *Ulmus* (collection no. 374)—the perithecia are distinctly beaked.

100μ
1

100μ
2


500μ
3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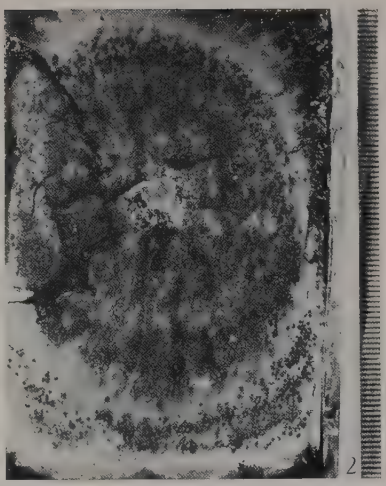
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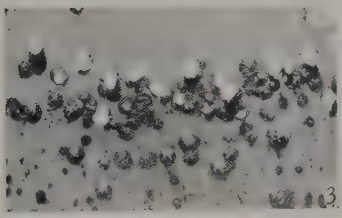
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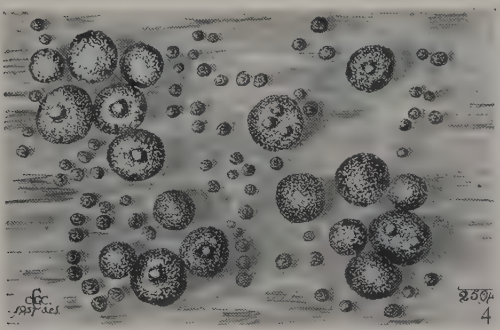
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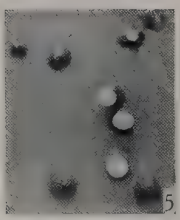
4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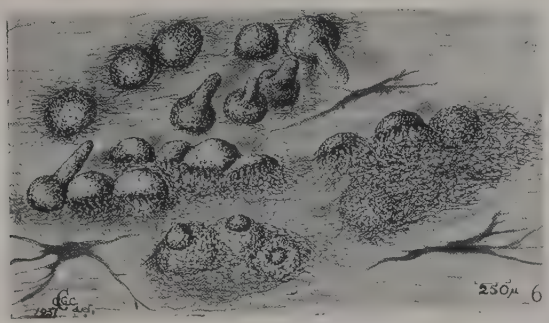
230µ
6

CONTRIBUTION TO THE BIOLOGY OF *COLLYBIA RADICATA* (RELH.) BERK.

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(With Plates VIII and IX)

Introduction

The long "rooting-base" with which the stipe of the common agaric, *Collybia radicata* (Relh.) Berk., is provided terminates, as Fries (1821) originally pointed out, in an attachment to a subterranean tree root and thus establishes the species as lignicolous although apparently terrestrial. There already exists an extensive literature dealing with this remarkable "root" and with the origin and development of the sporophores but, so far, there is no information available concerning the vegetative state of the fungus or its effect upon the tree roots.

The material used in this investigation was collected during the past three years, chiefly from a number of localities around Bristol. A number of isolated collections made in Great Britain, France and Germany have also been examined. On the discovery of a sporophore a careful examination was made of the tree root from which it arose and, when possible, isolations of the fungus in pure culture were made from the spores. In every instance numerous light brown lines were found in the wood of the infected root and sometimes a brown, paper-like tissue was found in the position of the cambium between bark and wood. A study of *C. radicata* was then undertaken to establish the exact relation and significance of these brown lines in the infected roots to this lignicolous species.

The pseudorhiza

The term "pseudorhiza" was introduced by Fayod (1889) to supplant those of "rooting base" and "root" previously applied to *C. radicata*. He points out that the application of such terms to fungi must lead to confusion, especially when the structure so designated arose by intercalary growth. He regards the pseudorhiza as part of the mycelium and as distinct from the reproductive organ, the sporophore, which it conveys to the surface of the ground.

In the original diagnosis of this fungus Relhan (1785 *a*) described the stipe as 4–6 in. high, gradually thickening from the pileus to the ground, then penetrating the earth in the form of a long root tapering

downwards. Later, he (1785 *b*) described a variety in which the stipe is less than 2 in. high and swollen to the size of a finger while the root is 14 in. long and large in proportion. I have found a complete range of pseudorhizae varying from 3 in. in length to the extreme example shown in Pl. VIII, fig. 1 where the stipe was only 2½ in. long and much less substantial than the 19 in. long pseudorhiza. It is clear that length of pseudorhiza is of little systematic importance, depending as it does upon the position of the infected root in the ground. Corner (1934) describes the pseudorhiza of this fungus as an opportunist growth, made when the primordial shaft has a considerable distance to cover before the pileus can be developed and is thus not a primary distinguishing character. I have observed that small sporophores are correlated with abnormal lengths of pseudorhizae. It must be recognized, however, that, as Greville (1826) pointed out, the singularly long pseudorhiza is a constant and peculiar character of this species. Lange's (1915) "rootless" form, *C. radicata f. arrhiza*, must in my opinion be regarded as a very unusual development under natural conditions. The pseudorhiza of *C. radicata* would seem to be best regarded as an ephemeral rhizomorph, adapted solely for the purpose of bearing a single sporophore at a suitably exposed position near the surface of the ground.

Infection of the roots

In September 1934 a preliminary attempt was made to infect roots of two mature, healthy oak-trees by wound inoculation. Twelve roots, about 6–8 in. under the soil, were uncovered and six of these were inoculated with spores and six with mycelium. The method adopted was to cut out a V-shaped slice from the root and place the spores or mycelium in the wound. The wedge of root was then replaced and held in position by a piece of sticking plaster. Control cuts were made at the time upon the same roots. The soil was then replaced on the roots and their positions marked by metal skewers. In July 1935, the roots were examined but there were no differences discernible in the inoculated and control wounds. Extensive browning occurred around all the wounds, due to "wound-gum" production, but no hyphae had penetrated beyond this area. In view of the negative nature of these results no further experiments were carried out, although field observations seemed to suggest that this fungus does, in certain circumstances, act as a wound-parasite.

The method of infection is obscure. Roots from which sporophores of *C. radicata* arise are virtually pure cultures from which the fungus can readily be isolated. It is very unusual to find another fungus present in the immediate neighbourhood of the *Collybia*, although on one occasion a beech-root was discovered with an additional infection

of *Ustulina zonata*, as evidenced by its black lines, and subsequent confirmation by culture. The normal habitat of the fungus in underground roots seems to require some method of spore transference other than the familiar air dispersal. It is possible that infection of a tree may sometimes occur at ground-level and the growth of the fungus be subsequently directed to the roots. However, all the present observations appear to negative this, since the roots are frequently found to be sound at points above the immediate area from which the sporophores arise. It may be that the spores are insect-borne; when a mature pileus of *Collybia radicata* is brought into the laboratory and left for a few days, it is invariably reduced to a mucilaginous mass by the larvae of dipterous insects. These insects undoubtedly eat the spores and may sometimes inoculate the tree with the fungus. A similar feeding on the spores by the large insect fauna of the forest floor, particularly beetles which can attack the bark, would supply a reasonable explanation of infection of underground roots. No direct evidence is available, but the facts that the spores are attractive to insects, are provided with a thick wall and are difficult to germinate under ordinary conditions, would rather suggest that this may be the method of infection.

Appearance of infected roots

The pseudorhiza of a sporophore of *C. radicata* was carefully followed through the soil, often with great difficulty as it was very brittle, until the root to which it was attached was uncovered. As large a portion of the root was dug out as was possible. Both oak and beech roots were examined and were found to differ in no particular so far as the infecting fungus was concerned. Externally, infected roots showed no sign of the presence of the fungus, except of course for the pseudorhiza. On removing the bark, which was usually intact, a brown, wrinkled plate appeared in the position of the cambium, between wood and bark. It was from this plate, or just beneath it, that the aggregation of mycelium forming the pseudorhiza originated. On sawing through the root, many light brown lines became visible at the cut surfaces, while it could also be seen that the brown tissue in the cambium encompassed the entire woody cylinder. The lines, as they appeared in a section of the root, were very thin, light brown with a darker central portion, from which the brown colour diffused into the surrounding wood. Their appearance is particularly characteristic of the fungus. In more rotted woods, the lines become thicker and darker but the same diffusion of brown colouring matter characterizes them. Brown lines were always plentiful in the root near the point of origin of the pseudorhiza but sometimes they vanished rapidly within a few inches; the root above the infection was ap-

parently quite sound. It often seemed that the fungus tended to produce localized diseased areas. If a piece of wood, free from brown lines, was cut from an infected root and allowed to dry out slowly under a bell-jar, a brown covering developed over the entire surface of the block. This experiment was repeated several times with the same result, the white wood slowly darkening until it became a dusty brown. On slicing off a piece of the wood, the brown surface coating appeared as a brown line in section, always situated some little distance back from the cut surface. It was found, too, that the area of white wood exposed became similarly covered by a brown coating at the end of a few days. Pl. VIII, fig. 7 shows a section of a piece of infected root which has been surrounded by the brown coating on being left under a bell-jar for about three weeks. Thin sections through the brown lines in the wood show that they are composed of densely massed hyphae, whose walls are commonly cemented together without interhyphal spaces and which entirely block the tracheides and medullary-ray cells in which they are found. These hyphae are very variable in size but all are characterized by the uniform deposit of brown pigment on the outer surface of the hyphal wall. This pigment diffuses for some distance from the hyphae, staining the walls and pits of the wood cells. Hyphae in the cells of the medullary-rays have an average diameter of 2 μ, while those found in the tracheides and vessels are much larger, having a diameter of 6–8 μ. Large, elongated, cells, with a length of 20–30 μ, are often to be found but, owing to the dense interlacing of the hyphae, the whole length of individual cells of the hypha can seldom be observed in a single section. Very delicate hyphae, 1–1·5 μ in diameter, which pass unconstricted from cell to cell by means of the pits, occur throughout the wood; these hyphae are particularly numerous and are responsible for the attack on the wood. The decay produced by the fungus is a "white rot" in which the wood-elements rapidly lose their ability to react with lignin stains. This delignification is complete only in old, disintegrating roots.

Growth in pure culture

The growth of *C. radicata* has been studied in pure culture on a variety of media through a number of sporophore generations. Originally, spore-casts of the fungus were obtained by setting up a pileus on a small glass ring in a sterile Petri dish. In this study, cultures derived from these spores, both of monospore and multispore origin and from isolations of the fungus from infected roots, have been employed. In the present paper the growth of multispore cultures is described and brief mention is made of monospore mycelia, in regard to the aversion shown between certain mycelia.

In the material studied, the spores of *C. radicata* were ellipsoid, averaging 12–16 × 10–11·5 μ, with thick prominent walls. Spores kept at room-temperature soon lose their viability so that, throughout, a practice has been made of keeping the spore-casts in a refrigerator at 5° C. Under these conditions, the spores remain viable for a period of four months or even more. Germination takes place slowly, mycelial growth being unusual in less than eleven to fourteen days. Once germination has occurred, mycelial growth is rapid and luxuriant at room temperature, reaching an optimum at about 26° C. In the initial growth, the hyphae have an average diameter of 3 μ and are provided with large clamp connexions 2·5 μ wide. The mycelium is pure white and forms a thick, fluffy growth. No oidia have been seen in the cultures.

Many different media have been employed for the growth of the fungus and, in general, it may be said that media with abundant and readily available carbohydrate are most suitable. Satisfactory mycelial growth with rapid sporophore production has been obtained on agars containing 4 or 6 % malt extract and upon sterilized bread moistened with 2 % malt extract. Dense mycelial growths have been produced on "C" (1) medium (Campbell, 1933) and on sterilized blocks of various woods such as oak, beech, horse-chestnut and ash, but without sporophore production.

On all media, the white mycelium rapidly covers the available surface; then, after a period varying from a fortnight to two months, brown areas begin to appear upon the mycelium. These may spread until, as in very old cultures, the whole surface of the medium is covered with a tough, brown layer of mycelium. Where masses of mycelium have filled the culture tube, brown lines are now seen which divide it up in an irregular manner. The cultures on malt agar show, usually after about one month, the presence of a brown plate extending from the surface mycelium down into the agar, eventually meeting the wall of the tube, as can be seen in Pl. IX, fig. 1.

On occasion these brown plates may form elaborate structures: a complete cylinder formed in this manner is shown in Pl. IX, fig. 2. The development of these brown plates is of considerable interest: at first a faint white plate is visible in the agar; this develops evenly over the whole area to be covered till, gradually becoming darker and more clearly defined, it eventually forms the dark brown plate.

The plate, although apparently so substantial, is rarely more than 40 μ thick. Its development has been followed by preparing and microtoming blocks of agar containing the line. The brown plate is the result of close branching of the intermeshing hyphae which form a homogeneous tissue without interhyphal spaces. The individual hyphae, which vary in diameter from 2 to 16 μ with an average of 6 μ, are usually cemented together by a deposit of brown refractive

material. The deposition of brown material on the cell walls is identical with the sclerotization of cells forming the rind of a typical sclerotium. The densest deposit, several microns in depth, of the sclerotizing substance occurs at the outer edge of the plate, as is clearly shown in Pl. IX, fig. 7. In this position the brown deposit has a cuticular function forming an impermeable and protective layer for the palisade of hyphae.

When mycelia of multispore origin, each derived from different sporophores, are grown together upon the same substratum, marked aversion is almost always exhibited by the paired mycelia. When however the mycelia are compatible, they intermingle completely, producing a uniform felt over the substratum. Similar results are obtained by pairing monospore mycelia derived from different sporophores. A typical example of aversion is shown in Pl. IX, fig. 5 where two multispore mycelia were established on malt agar in a Petri dish. Eventually, the mycelia met in the middle of the dish and in a few days a marked aggregation appeared on each opposing mycelium some distance back from the point of contact. A brown pigmentation of the aggregations next took place, accompanied by a copious exudation of a clear fluid, in all recalling the formation of sclerotia in culture. Then a brown plate became evident, stretching from the aggregations down into the agar to make contact with the glass, thus forming two barriers between which was left a portion of the medium, bearing very scanty mycelium and apparently abandoned by the averting mycelia (Pl. IX, fig. 6). This derelict area varies greatly in width from 2 to 40 mm. in different cultures. Pl. IX, fig. 7 represents a section through one of the brown walls which is composed of sclerotized, swollen hyphae, such as have been previously described. The brown plates, whether formed in a single mycelium culture (Pl. IX, figs. 1, 2 and 8) or in a culture with two averting mycelia (Pl. IX, fig. 6), are identical in structure.

There is considerable literature dealing with aversion manifested by both haploid and diploid mycelia of the same species. A number of terms, such as "barrage", "inhibition" and "lines of demarcation", have been employed to describe phenomena which appear to be similar to the aversion shown by mycelia of *C. radicata*, but it is not to be inferred that they are identical phenomena, dependent upon the same circumstances. Indeed, there is much to suggest that, within the apparent similarity, a number of entirely different phenomena occur in different species. However, the phenomena described by Mounce (1929) and Cayley (1923) seem to bear a very close resemblance to those observed in *C. radicata*. Mounce found aversion between both monospore and multispore mycelia of *Fomes pinicola*, resulting in a "line of demarcation" where the two averting mycelia meet. This "line" is "jet-black, tough and almost sclerotial-like in

character". Cayley has dealt very fully with aversion between monospore mycelia of *Diaporthe perniciosa*, showing that a thick-walled, stromatic, protective growth of mycelium forms at the edge of each colony on either side of the line of contact. Apparently from her figure, Pl. XX, fig. 9, the stromatic walls are formed down into the medium in a manner very similar to those of *C. radicata*, shown in Pl. IX, fig. 6. It is sufficient to note here that both these authors remarked upon the stromatic, sclerotial-like character and the protective nature of the opposing edges of the averting mycelia.

A large number of sporophores have been produced in the cultures, chiefly on malt-agar slopes. These were very variable in size with stipes from 1 to 7 cm. in length, average 4 cm., and pilei 1–3 cm. in diameter, average 1·2 cm. All produced viable spores of the same size range as those found in nature. In recently isolated mycelia the sporophores usually appeared about three weeks after inoculation, while in older mycelia much longer periods were necessary and in many cultures no sporophores were produced at all, even after two years' growth. Two groups of sporophores are shown in Pl. IX, figs. 3, 4 growing on 2 % malt-agar slopes. In each case the sporophore-initials were first formed below the brown mycelial plate on the surface of the culture, part of which has been torn by the elongation of the sporophore. It seems that light is not necessary for sporophore production, since a number of sporophores appeared in cultures kept in the dark. This fact observed in culture evidently has its equivalent in nature, as an abnormal sporophore was discovered buried some 8 in. under the earth surrounding a beech tree, from the roots of which it had arisen. This sporophore, which was pure white with a fully expanded pileus and a much-coiled and twisted stipe, had apparently been formed in a small pocket in the ground about 6 in. in diameter, in which confined space the elongation of the stipe had brought about its coiled condition.

In one of the cultures a large, white hump appeared, from which ultimately grew out a number of gills, so that the whole seemed not unlike an inverted pileus; in another were formed yellow, gilled growths, in appearance recalling a *Tremella* fructification. Neither of these structures bore basidia or spores although they were undoubtedly attempts at sporophore-formation.

Significance of the brown line

It has been shown that the brown plates, or lines as they appear in section, are a constant feature of tree roots infected by *C. radicata*. The plate in the position of the cambium completely encompasses the wood cylinder while others divide it into irregular portions. The

formation of these plates can be induced around a piece of infected wood, which has hitherto been without them, by allowing the wood to lose water gradually by placing it under a bell-jar. This suggests that they protect the mycelium in the wood against desiccation and possible invasion by other fungi. The structure of the line bears out this interpretation as it is composed of densely massed hyphae which have undergone sclerotization to form a compact tissue identical with the rind of a typical sclerotium. In general, sporophores which arise from true sclerotia have their origin below the rind: it is significant, therefore, that the sporophore initials of *C. radicata*, developed in culture, should originate beneath the brown plate, through which they eventually burst. From both functional and morphological standpoints, the brown plates may be regarded as equivalent to the rind of a sclerotium, the medulla of which is buried in the wood tissues: such a sclerotium, naturally, consists largely of wood elements and for such an entity the term pseudosclerotium has been proposed.

Summary

The sporophores of *C. radicata* are remarkable in that they arise from tree roots often buried several inches under the ground. The vegetative mycelium of the fungus produces a white rot in the wood of infected roots by extensive and rapid delignification. A prominent feature of infected roots is the presence of brown plates, or lines, as they appear in section, in the wood. These plates are composed of large, many branched hyphae forming a compact tissue in which individual cells are cemented together by a brown substance. This substance diffuses some distance into the wood, staining tracheide walls and pits in a characteristic manner. The substance seems to be identical with that which causes the sclerotization of the hyphae forming the rind of a sclerotium.

The development of the fungus in pure culture on a number of media has been studied. Sporophores producing viable spores have been formed in these cultures. Aversion is evident between a number of mycelia of both monospore and multispore origin when grown on the same substratum. Such averting mycelia develop tough, brown plates in the medium, thus effectively separating the opposed mycelia. These plates are identical in structure with those found in infected roots and comparable in both structure and function with the rind of a sclerotium, the medulla of which is composed of hyphae within the wood. The term pseudosclerotium has been suggested to distinguish this structure from the true sclerotium.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

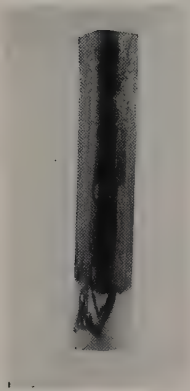

Fig. 5

Fig. 6

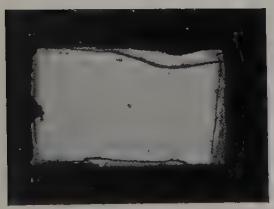

Fig. 7

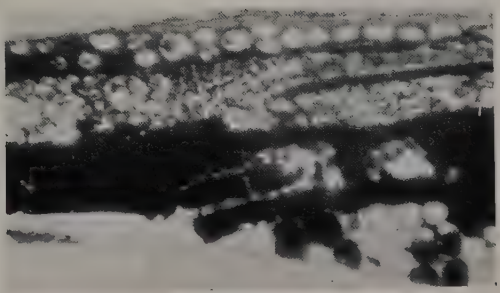

Fig. 8

Fig. 1

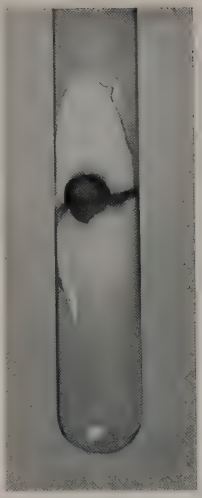

Fig. 2

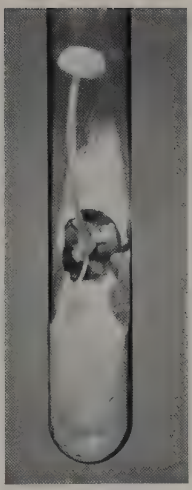

Fig. 3

Fig. 4

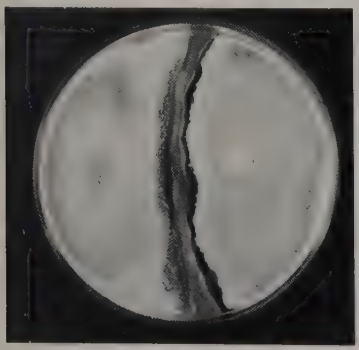

Fig. 5

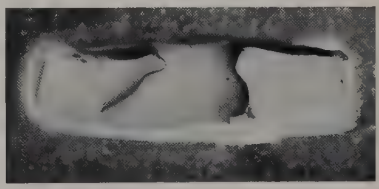

Fig. 6

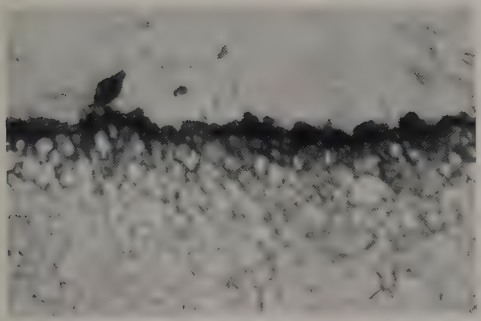

Fig. 7

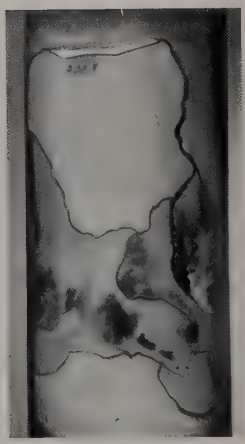

Fig. 8

REFERENCES

Campbell, A. H. (1933). "Zone lines in plant tissues. I. The black lines formed by *Xylaria polymorpha* (Pers.) Grev. in hardwoods." *Ann. appl. Biol.* xx, 123.

—— (1934). "Zone lines in plant tissues. II. The black lines formed by *Armillaria mellea* (Vahl) Quél." *Ann. appl. Biol.* xxi, 1.

Cayley, D. M. (1923). "The phenomenon of mutual aversion between monospore mycelia of the same fungus (*Diaporthe perniciosa* Marchal) with a discussion of sex heterothallism in fungi." *J. Genet.* xiii, 353.

Corner, E. J. H. (1934). "An evolutionary study in Agarics: *Collybia apalosarca* and the veils." *Trans. Brit. mycol. Soc.* xix, 39.

Fayod, V. (1889). "Prodrome d'une histoire naturelle des Agaricinés." *Ann. Sci. nat.* Sér. 7, ix, 214.

Fries, E. (1821). *Systema Mycologicum*, i, 118.

Greville, R. (1826). *Scot. Crypt. Flora*, iv, t. 217.

Lange, J. E. (1915). "Studies in the Agarics of Denmark, II." *Dansk. Bot. Ark.* ii, 15.

Mounce, I. (1929). "Studies in forest pathology. II. The biology of *Fomes pinicola* (Sw.) Cooke." *Dept. Agri. Canada Bull.* No. 111, New series.

Relhan, R. (1785*a*). *Flora Cantabrigiensis*, p. 529.

—— (1785*b*). *Flora Cantabrigiensis*, Suppl. ii, 25.

EXPLANATION OF PLATES VIII AND IX

All figures refer to *C. radicata*

Plate VIII

Fig. 1. Sporophore with a short stipe and abnormally thick pseudorhiza which is 19 in. long. × $\frac{1}{8}$.

Fig. 2. Sporophore with average-length pseudorhiza. × $\frac{1}{5}$.

Fig. 3. Section of beech root showing the brown lines. × $\frac{3}{4}$.

Fig. 4. Portion of beech root from which the bark has been removed. The brown wrinkled plate is visible in the position of the cambium. × $\frac{3}{4}$.

Figs. 5, 6. Horse-chestnut roots infected by the fungus in pure culture. Note the brown superficial plate and the lines in the wood. × $\frac{1}{2}$.

Fig. 7. Section through piece of root which developed superficial plates upon slowly drying out under a bell-jar. Note that the plates have been developed a short distance from the cut surfaces. × $\frac{3}{4}$.

Fig. 8. Longitudinal transverse section of beech root through a brown line. Note the packed hyphae in the wood cells and the pigment infiltrating the pits. × 230.

Plate IX

Fig. 1. Two months old culture showing mycelial plate developed down into the agar. × $\frac{3}{4}$.

Fig. 2. Three months old culture with a cylindrical body formed by the brown plate making contact with the wall of the tube. × $\frac{3}{4}$.

Figs. 3, 4. Groups of sporophores developed in pure cultures. The brown sclerotic plates on the surface of the medium have been broken by the elongation of the sporophore initials which originated beneath them. Note the spore-casts on walls of tubes. × $\frac{3}{4}$.

Fig. 5. Two averting mycelia of multispore origin which have formed sclerotic walls on the opposed mycelia. A clear area of medium can be seen between the boundary walls. Description in text. × $\frac{1}{2}$.

Fig. 6. A section of the culture shown in the previous figure in which the sclerotic walls can be seen to extend down into the medium. × 6.

Fig. 7. Part of the sclerotic wall showing the pseudo-parenchymatous structure and the dense deposit of sclerotizing material on the outside. × 550.

Fig. 8. Three months old culture on a beech root showing the superficial mycelium divided and bounded by the brown plates. × $\frac{3}{4}$.

OBSERVATIONS OF THE AQUATIC FUNGI OF THE ABERYSTWYTH DISTRICT

By ETHEL M. BROWN

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(With 1 Map and 2 Text-figures)

From September 1935 to February 1936, a study was made of the aquatic fungi occurring in pools and lakes around Aberystwyth. Collections were made from each pool about once a month. Water from the pool, containing submerged twigs, leaves, or other debris, was brought into the laboratory, and from this cultures of the various fungi were obtained.

Topographical account of the area studied

The area in which the study was made extends about seven miles north of Aberystwyth, and four miles south and about nine miles inland (see Map).

At its inland limit the area includes a portion of the high plateau at about 1000 ft., in which individual peaks rise to a height of about 1500 ft. This plateau falls gradually on the western side towards the coastline, but the coastal plain is interrupted by portions of a second plateau of about 250 ft., which in places extends to the coast, forming cliffs.

The area is intersected by several rivers, the general direction of their flow being westerly. The upper parts of most of the river valleys are narrow with steep sides, but towards the sea they widen, merging into the coastal plain.

General ecology of pools studied

The pools and lakes which were investigated fall into three main groups,—those which occur on the high plateau at a height of about 1200 ft., those occurring near sea-level, either near the sea or beside the river, and those at an intermediate height on the coastal plateau.

The mountain pools studied were disused reservoirs, having a shaley substratum, and very clear water with practically no macrophytic vegetation. The pools referred to as J, L and M constitute this group. These pools receive drainage from the high plateau where the vegetation is mainly of the moorland type. Above the tree limit, at about 1000 ft., the area consists largely of grassy sheep walks, the

Map of area showing ponds studied.

flora consisting mainly of *Festuca ovina*, *Molinia caerulea*, and *Nardus stricta*. Sometimes in moister conditions bog plants occur, such as *Sphagnum* spp., *Drosera rotundifolia*, *D. longifolia*, *Pinguicula vulgaris* and *Juncus squarrosus*, and on rather drier ground *Calluna vulgaris*, *Vaccinium Myrtillus*, and in some places several species of *Lycopodium*.

The pool E was at an intermediate altitude of 500 ft. It was a marshy pond in a sheep pasture. The pond was surrounded by a fringe of *Juncus communis*, and contained *Potamogeton natans*, *Lemna minor*, and other water weeds. The water was deep and clear, although the substratum was muddy.

The third group consists mainly of marshy ponds on the flats of the River Rheidol. Ponds B, C and D were of this type. They all had a rich vegetation consisting of water weeds such as *Alisma Plantago-aquatica*, *Ranunculus aquatilis*, *Potamogeton natans* and *Lemna minor*, and were surrounded by marshy grass land with tufts of *Juncus communis*. Pond B was close to a farm, and cattle were frequently seen grazing around it.

The ponds almost at sea-level also include A, which was a small stream of slow-flowing water. The stream had a rocky bed, the alga *Batrachospermum* being found on the stones. At the point at which collections were made, the stream flowed through a small wood, decaying leaves and twigs, therefore, occurred abundantly in the water.

G was a small roadside ditch of very muddy water, covered with *Lemna minor*. This ditch was almost at sea-level, and was near the sea.

F was a marshy pond at sea-level, on the Borth Golf Links, and it is possible that the fungi found in this pond were affected by the saline conditions.

Methods of making cultures

Rough cultures were first obtained from the natural waters of the pools by baiting in various ways. Ants' eggs, cress seeds, rose hips and dead flies were used as bait. The waters from the ponds were placed separately in sterilized Petri dishes. The bait was sterilized by boiling and a single piece of bait was placed in each dish. The dishes were kept in a cold room to prevent, as far as possible, growth of bacteria.

After a few days a visible mycelial growth developed on the bait, hyphae being seen radiating from it, and sporangia began to develop. At this stage, subcultures were made in order to obtain the fungus free from bacteria and protozoa.

For the subcultures tap water was sterilized and subsequently aerated by bubbling air through it. Fresh sterilized dishes were taken, and the water was placed in the dishes with pieces of fresh sterilized

bait. A small piece of mycelium from the original bait was then transferred to the fresh water, using forceps and needles, which had been sterilized by passing through a flame.

Subculturing, by this method, was repeated several times, until clean cultures, free from bacteria and Protozoa were obtained.

It was possible that, in these cultures, several species might be present on a single piece of bait. It was, therefore, necessary to obtain pure cultures before the species could be properly identified.

Some of the pure cultures were obtained by teasing out a single sporangium under the microscope, with needles, and transferring it to fresh culture dishes with fresh bait. By this method, zoospores from a single sporangium would be liberated and grow on the fresh bait, thus ensuring a pure culture of a single species. This method was satisfactory in some cases, but the separation of a single sporangium was rather difficult by such a rough method.

A second method was therefore sometimes employed to obtain pure cultures. The fungi were grown in water, subcultures being made until clean cultures were obtained and then, at the stage when they were producing sporangia abundantly and liberating zoospores, the water in which they were growing, containing zoospores, was diluted about five times and was then sprayed through a very fine nozzle on to a sterilized plate of pea agar. By the spraying, zoospores were distributed on the agar plate, and as soon as the spores began to grow, after about two days, the infected portions of agar were transferred to separate clean agar plates. By this means, single spore infections were obtained on the agar plates.

When a considerable mycelial growth was produced in the agar, and reproductive organs began to be formed, the fungus was transferred to sterilized water again, where better growth and production of sexual organs took place.

Portions of the agar containing the fungus were placed in sterilized dishes of water containing the original kind of bait.

Some species were produced directly from twigs brought into the laboratory from the pools. Waterlogged twigs were collected and were washed and placed in jars of sterilized tap-water, a single twig being placed in each jar. The water was changed every day, until a visible growth developed, and then changed every two or three days.

List of species found

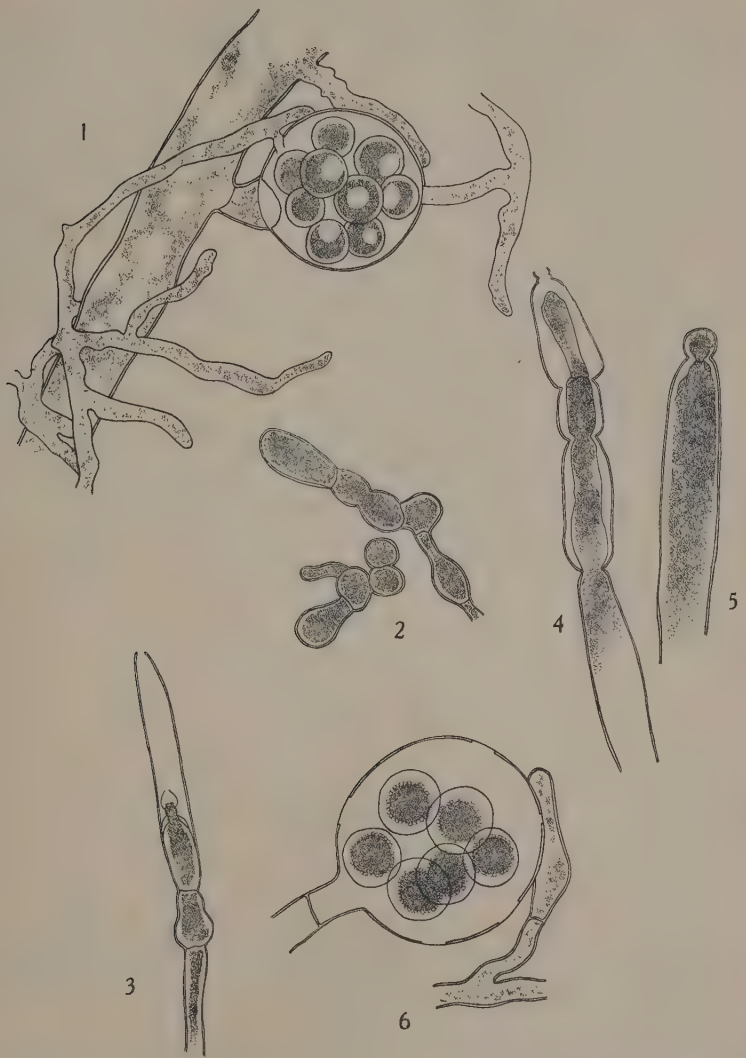
I. *Saprolegnia monoica* Pringsheim (Coker, Pl. 13). In D and J.

Both sporangial and sexual stages of the fungus were found. The sporangia are typical of *Saprolegnia*, showing proliferation from within. Oogonia were observed with both androgynous and diclinous antheridia. Numerous gemmae also occurred in older cultures.

II. *S. crustosa*, var. II. In. A.

Sporangial and oogonial stages were seen, the sporangia showing liberation of the spores and proliferation from within. The oogonia occur in clusters, with numerous diclinous antheridial branches. Clusters and chains of gemmae were also seen.

Text-fig. 1. *Saprolegnia paradoxa*. 1, oogonium containing numerous eggs, centric, with conspicuous oil drops; ×331. 2, 7, spherical oogonia; ×91. 3, 5, cylindrical oogonia, containing many eggs; ×91. 4, club-shaped oogonia; ×91. 6, 8, intercalary oogonia; ×91.



Text-fig. 2. *Saprolegnia crustosa.* 1, oogonium with mature eggs and androgynous and diclinous antheridia; ×385. 2, gemmae; ×95. 3, sporangia showing proliferation; ×190. *Saprolegnia mixta.* 4, sporangium showing proliferation; ×255. 5, young sporangium; ×255. 6, mature oogonium with pitted walls and ripe eggs, and antheridia; ×385.

III. *S. ferax* Thuret (Coker, Pls. 11, 12). In F (sea-level).

Typical sporangia were found. Oogonia were numerous and characterized by pitted walls. Antheridia were infrequent, being androgynous when present.

IV. *S. mixta* de Bary. In M (1150 ft.).

This species is similar to *S. ferax*, but it has fewer and larger eggs in the oogonium, and antheridia were present on about half the oogonia. Gemmae were also produced.

V. *S. paradoxa* Maurizio. In G (sea-level).

No sporangia were found in this species, but oogonia were abundant and of various shapes, being frequently intercalary. No antheridia were seen and no gemmae were formed.

VI. *S. delica* Coker (Coker, Pls. 5, 6). In C.

Numerous sporangia were found showing proliferation from within in the normal manner, and also frequently from below, as in *Achlya*. Oogonia were numerous, in clusters. Numerous antheridia, both androgynous and diclinous, were found, and gemmae were also abundant.

VII. *Achlya racemosa* Hildebrand (Coker, Pl. 31). In B and C (near sea-level), and also in L (1075 ft.).

The sporangia were of typical *Achlya* type and the oogonia were borne in a racemose arrangement with androgynous antheridia. No gemmae were found.

VIII. *A. colorata* Pringsheim (Coker, Pl. 32). Grown from twigs collected from B.

Typical sporangia were found and oogonia similar to those of *A. racemosa* but with papillae on the walls. Androgynous antheridia were present. No gemmae were produced.

IX. *Isoachlya toruloides* Kauffman & Coker (Coker, Pl. 31). In E (500 ft.).

Sporangia were found, proliferating either from within as in *Saprolegnia* or sometimes laterally from below as in *Achlya*. Oogonia were found, being frequently intercalary, or in chains. No antheridia were found. Some gemmae were produced.

X. *Apodachlya* sp. (Coker, Pl. 59). In M and was also grown from twigs from B.

The species from the two localities appeared to differ slightly in the shape and size of the sporangia and spores. No sexual organs were found in either sample.

XI. *Leptomitus lacteus* Agardh (Coker, Pl. 58). In B.

Sporangia were found containing a single row of spores which escape as in *Saprolegnia*, but new sporangia are formed in basipetal succession. The characteristic constrictions in the hyphae were seen. Sexual organs have never been found.

This work was done in the Botany Department, University College, Aberystwyth, under the direction of Dr I. M. Wilson, whom I thank for help and advice.

REFERENCES

Barnes, B. & Melville, R. (1933). "Notes on British aquatic fungi." *Trans. Brit. mycol. Soc.* xvii, 82.

Coker, W. C. (1923). *The Saprolegniaceae, with notes on other Water Molds.* Univ. of North Carolina Press.

Cook, W. R. I. & Forbes, E. J. (1933). "Investigations on aquatic fungi." *Nature, Lond.*, cxxxii, 641.

Forbes, E. J. (1934). "Observations on some British water moulds (Saprolegniales and Blastocladiales)." *Trans. Brit. mycol. Soc.* xix, 221.

Sparrow, F. K. (1933). "The Monoblepharidales." *Ann. Bot., Lond.*, xlvii, 517.

Thaxter, R. (1895*a*). "New or peculiar aquatic fungi. I. *Monoblepharis*." *Bot. Gaz.* xx, 433.

—— (1895*b*). "New or peculiar aquatic fungi. II. *Gonapodya* Fischer and *Myrioblepharis* nov. gen." *Bot. Gaz.* xx, 477.

—— (1896). "New or peculiar aquatic fungi. III. *Blastocladia*." *Bot. Gaz.* xxi, 45.

NOTE ON THE SUPPOSED CONNEXION BETWEEN *MASTIGOSPORIUM ALBUM* RIESS AND *DILOPHOSPORA ALOPECURI* (FR.) FR.

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(With 24 Text-figures)

Mastigosporium album Riess (Fresenius, 1852) is a Hyphomycete which causes brown or purplish coloured lesions on the leaves of *Alopecurus pratensis*. The somewhat sparsely produced conidia form a minute white centre to the spot. They are 3–4-septate, measure 40–62 μ and carry long thin appendages at the apex and sometimes at the upper septum. The fungus is not uncommon in England, and Miss Wakefield (1918) recorded a muticate variety on *Dactylis glomerata*. We have found this form on *Agrostis alba* in Wales.

Since 1921 *Mastigosporium album* and its variety *muticum* have been observed annually at the Welsh Plant Breeding Station on the hosts mentioned above. The disease may be found throughout the year, but the attack is often especially severe in late autumn and early spring. The only effect on the host is the spotting referred to above, which may, however, be sufficiently severe on *Alopecurus pratensis* to cause some damage to the crop.

Dilophospora Alopecuri (Fr.) Fr. (Sphaeropsidales), first recorded as *Sphaeria Alopecuri* by Fries (1828), occurs on a number of species of the Gramineae, including cereals as well as grasses. Berkeley (1862) described a very bad attack on wheat in England. In recent years it has been recorded on wheat but not to any serious extent (Ministry of Agriculture and Fisheries, 1925–27; 1928–32). It is, however, not uncommon on species of *Holcus* and on *Alopecurus agrestis*.

The effects of *Dilophospora* are much more striking than those of *Mastigosporium album*. The flowering shoot is twisted and malformed, and finally enveloped in a black stromatic mass in which are embedded the pycnidia. Infected shoots rarely produce flowers. The pycnidia are minute (120–300 μ), and the spores measure $12 \times 2{\cdot}2\ \mu$. They are septate and have several branched appendages at each end, which, according to Atanasoff (1925), possess a biological significance, becoming attached to eelworms which convey the fungus into the plant. That eelworms are necessary for infection was not supported by the observations of Schaffnit and Wieben (1928).

Fuckel (1869) suggested that *Mastigosporium album* and *Dilophospora Alopecuri* might be two stages of the same fungus, linking them at the

same time with the Ascomycete *Dilophia graminis* (Fuck.) Sacc. Atanasoff (1925) and others have doubted the connexion but recently Rainio (1936) claimed to have established the relationship of the two imperfect species by culture and inoculation experiments.

At Aberystwyth, we have failed over a period of seventeen years to find any evidence in the field of a connexion between *Mastigosporium album* and *Dilophospora Alopecuri*; in culture they seem to be completely unlike each other. In 1937 the following isolations were made and compared on artificial media in test tubes and plates: *Mastigosporium album* from *Alopecurus pratensis*; *Mastigosporium album* var. *muticum* from *Dactylis glomerata* and from *Agrostis alba*; *Dilophospora Alopecuri* from

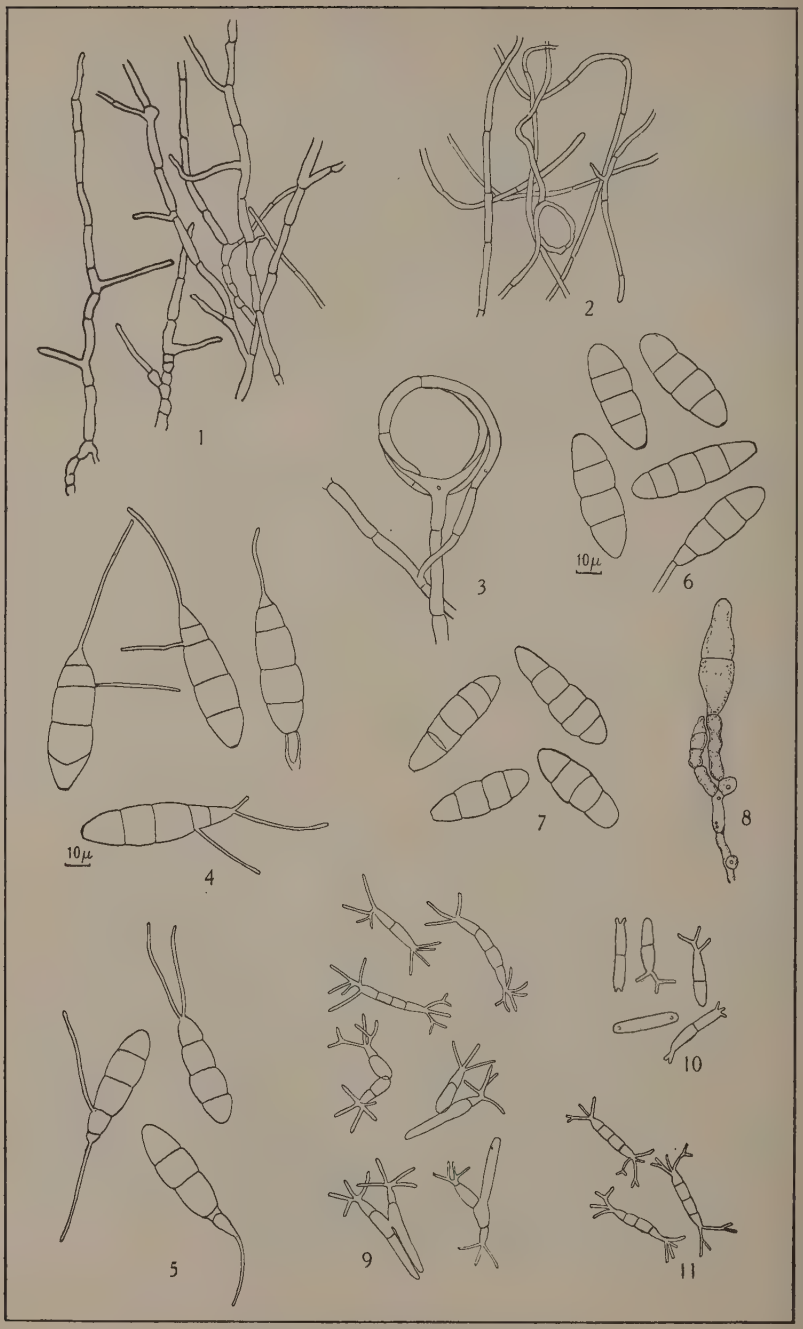
Table I. *A comparison of* Mastigosporium album *Riess and* Dilophospora Alopecuri *(Fr.) Fr. in culture. Plate cultures on potato-dextrose agar*

	Mastigosporium album and *M. album* var. *muticum*	*Dilophospora Alopecuri*
Rate of growth	Slow. Diameter 1 cm. in 3 weeks	More rapid. Diameter 3½ cm. in 3 weeks.
Surface	Yellow-ochre.* Moist owing to heaps of conidia which give the effect of a bacterial colony. Traces of white aerial mycelium only in old cultures, none developed for first few weeks	White at first when the colony is covered with a dense growth of cottony aerial mycelium. In older colonies the dark submerged mycelium can be seen
Reverse	Brighter in colour approaching light cadmium*	Olivaceous black (1)*
Shape of colony	Irregularly lobate	Circular
Sporulation	Superficial conidia very abundant	None
	Pycnidia absent	Pycnidia minute, dark (not black) spherical, scattered, superficial. Plentiful in old cultures

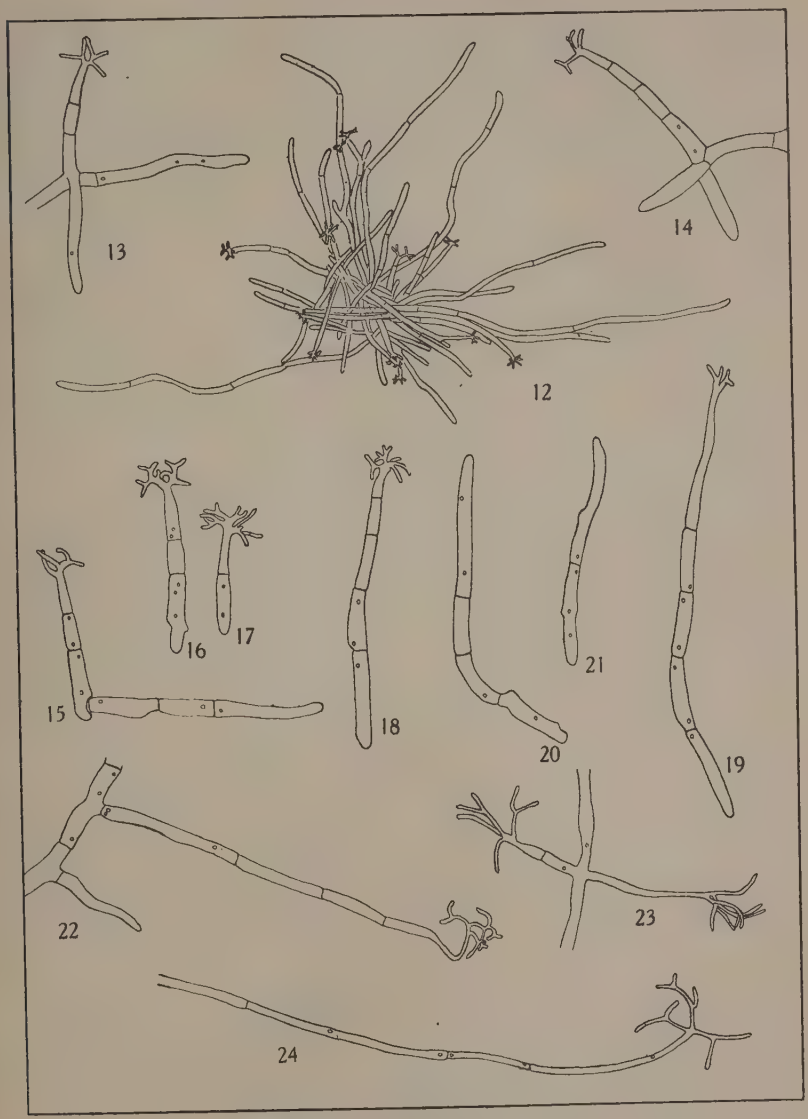
* *Color Standards and Color Nomenclature*, Robert Ridgway, Washington, 1912.

Holcus lanatus and from *Alopecurus agrestis*.† The results have been summarized in Table I. The different isolations of *Dilophospora Alopecuri* are practically identical. Those of *Mastigosporium album* and its variety agree closely in salient features, differing very slightly in the shade of colour and in the margin of the colony on a plate. The two species, however, present most striking differences in culture, varying widely in colour, growth rate and type of mycelium (Figs. 1, 2) and each produces freely its characteristic spore. In *Mastigosporium album*, conidial formation begins in colonies a few days old and is so prolific that moist confluent heaps always cover the surface of the yellow contoured growth. The conidia are identical with those produced in nature on the host and the appendaged and muticate

† The authors thank Dr A. Smith, Plant Pathological Laboratory, Harpenden, for fresh material of *Dilophospora Alopecuri* on these hosts.



Figs. 1–11. For explanation see p. 172.



Figs. 12–24. For explanation see p. 172.

forms maintain this distinction in culture (Figs. 5, 7). *Dilophospora Alopecuri* on the other hand develops a flat circular mycelial growth with abundant white aerial hyphae and dark submerged mycelium.

The development and the germination of the pycnidiospores of *Dilophospora* are interesting and have been previously described (Atanasoff, 1925; Bessey, 1916). Observations on immature pycnidia suggest that the appendages and septa develop when the young spores are lying free in the pycnidium (Fig. 10). On germination the two middle cells swell and separate, and from one, or both, germ-tubes grow out (Fig. 9). In young colonies many of the branches terminate in apical appendages like those found on the pycnidiospore (Fig. 12). Growth is often resumed by two branches which arise at some distance below the apex giving the effect of a cross (Figs. 13, 14). Several authors (Atanasoff, 1925; Schaffnit & Wieben, 1928; Rainio, 1936) have mentioned the occurrence in culture of secondary conidia and it seems clear from their drawings that they referred to these appendaged branches which separate somewhat easily when a young colony is taken from agar and mounted in water under a cover slip. The method of disarticulation is shown in Fig. 15. It occurs at the angle made by a lateral branch but it is not confined to those hyphae which bear appendages (Figs. 20, 21). At this stage the colony breaks up rather readily into fragments which vary considerably in length (Figs. 15–19). In older cultures also appendages may be found on short or long branches of the mycelium but disarticulation does not usually take place (Figs. 22–24). It is interesting that appendages are not confined to the pycnidiospores and their development might be a useful diagnostic feature in sterile cultures. Spiral coils (Fig. 3) are also characteristic of this fungus in culture.

In view of their wide variability in form and behaviour it is doubtful if the appendaged branches can be correctly described as secondary conidia. In colonies a few weeks old, pycnidia are freely produced on the surface of the agar medium. They contain viable pycnidiospores similar to those found on the living plant (Figs. 9, 11). No spore forms intermediate between *Mastigosporium album* and *Dilophospora Alopecuri* have been seen by us and it is exceedingly difficult to accept a genetical connexion between two such widely different types.

EXPLANATION OF TEXT-FIGURES

Fig. 1. Mycelium from a culture of *Mastigosporium album* from *Alopecurus pratensis*. ×275. All the drawings of figures were made under a camera lucida.
Fig. 2. Mycelium from a culture of *Dilophospora Alopecuri* from *Alopecurus agrestis*. ×275.
Fig. 3. Spiral hyphae of the same. ×675.
Figs. 4, 5. Conidia of *Mastigosporium album* from *Alopecurus pratensis*; (4) produced on host, (5) produced in culture. ×400.
Figs. 6, 7. Conidia of *Mastigosporium album* var. *muticum* from *Dactylis glomerata*; (6) produced on host, (7) produced in culture. ×400.

Fig. 8. Young conidium developing from the mycelium of *Mastigosporium album* var. *muticum* in culture. × 400.

Figs. 9–11. Pycnidiospores of *Dilophospora Alopecuri* from *Alopecurus agrestis*; (9) taken direct from host and kept for 24 hr. on agar, (10) developing spores from an immature pycnidium produced in culture, (11) mature spores produced in culture. × 925.

Fig. 12. Monospore colony of *Dilophospora Alopecuri* four days old on malt agar at 21° C., showing appendaged branches. × 400.

Figs. 13, 14. Side branches produced on an appendaged branch. These frequently grow in the opposite direction to the parent branch and produce the criss-crossed effect seen in the young colony (Fig. 12). × 925.

Figs. 15–21. Fragmentation in a colony of *Dilophospora Alopecuri* 7 days old on malt agar at 21° C. × 925.

Figs. 22–24. Appendages on mycelium taken from a culture 23 days old on oatmeal agar. × 925.

REFERENCES

Atanasoff, D. (1925). "The *Dilophospora* disease of cereals." *Phytopath.* xv, 11–40.

Bessey, E. A. (1916). "*Dilophospora Alopecuri.*" *J. Mycol.* xii, 57–8.

B[erkeley], M. J. (1862). "*Dilophospora graminis*, Desmazieres." *Gdnrs' Chron.* pp. 1009–10.

Fresenius, G. (1850–63). *Beitr. Mykol.* Frankfurt, pp. 56–7.

Fries, E. (1828). *Elenchus fungorum*, II, 90.

Fuckel, L. (1869). "*Symbolae mycologicae.*" *Beiträge zur Kenntniss der Rheinischen Pilze*, p. 130.

Ministry of Agriculture and Fisheries, London. "Fungus and allied diseases of crops 1925–7." *Misc. Publ. Bd Agric. Fish., Lond.*, No. 7, p. 12.

—— "Fungus and other diseases of crops 1928–32." *Bull. Minist. Agric., Lond.*, No. 79, p. 14.

Rainio, A. J. (1936). "Über die *Dilophospora*-Krankheit von *Phleum pratense* L. und *Alopecurus pratensis* L." *Valt. Maatalousk. Julk.* No. 87, pp. 1–32.

Schaffnit, E. & Wieben, M. (1928). "Untersuchungen über den Erreger der Federbuschsporenkrankheit *Dilophospora Alopecuri* (Fr.) Fr." *Forsch. PflKr., Berl.*, v, 5–38.

Wakefield, E. M. (1918). "New and rare British fungi." *Kew Bull.* No. 7, p. 233.

THE TAXONOMY OF FUNGI OF BLUE-VEINED CHEESE

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(With Plate X)

From 1906 to 1930 varied descriptions of blue cheese moulds have appeared in the literature. The earlier continental work of Weidemann (1907), Westling (1911), Sopp (1912), Biourge (1923) and Arnaudi (1927) showed a strong tendency to create new species based on minor colony differences but without due regard to the permanency of such differences. More recently, however, Thom (1930) has concluded that all moulds effecting the marbled appearance of blue cheese are strains of *Penicillium roqueforti* Thom which might display a multiplicity of intergrading forms. On closer inspection of many papers one finds that new species have been established on the examination of a limited number of cheeses, and consequently the authors have often failed to appreciate the gradation of form by comparison of many strains of the same group.

The object of this study was to establish whether or not moulds of blue-veined cheese are distinguishable *inter se*.

Experimental

Source and development of cultures

All types of blue-veined cheese obtainable in London were examined, representing a total of twenty different cheeses. The following types were obtained from reputable sources: seven samples of Stilton, three of Blue Cheshire, two of French Roquefort, one of Wensleydale, one of Danish Roquefort, two of Gorgonzola, two of Blue Vinney and two of Dolce Verde.

A standard technique for the isolation of the dominant mould was used with each sample. The cheese as supplied, generally in the form of a boring taken through its central portion with a sterile borer, was cut with a sterile scalpel under cover of a sterile Petri dish. From the newly exposed inner surface of the cheese a barely visible amount was removed from a blue vein with a strong wire and emulsified in a tube of melted beer-wort agar cooled to 45° C. The first plate was poured from this tube. Retaining the original tube for mixing, seven more

dilution plates were prepared. After five to seven days' incubation at 24° C. the dominant mould was subcultured from a discrete colony. Further purification was effected by making single spore cultures of each of the dominant moulds.

Media

Four media were chosen for the cultivation of the moulds:

(1) Beer-wort agar. Supplying conditions for luxuriant growth.

(2) Czapek Dox agar (Thom).

(3) Inorganic A agar. A medium not supporting optimal growth, but serving to separate the more robustly growing strains from the more delicate.

(4) Organic C agar. A medium suppressing spore production by *P. roqueforti* Thom but inducing the formation of a stellate colony. The medium is of diagnostic value in that the mycelial pattern can be readily appreciated in the absence of a dense sporing felt.

Formulae of media

(1) *Beer-wort agar:* beer wort s.g. 1·04; agar agar 2 %; *p*H 3·9.

(2) *Czapek-Dox agar* (Thom): Sodium nitrate ($NaNO_3$), 3·0 g.; dipotassium hydrogen phosphate (K_2HPO_4), 1·0 g.; magnesium sulphate ($MgSO_4.7H_2O$), 0·5 g.; potassium chloride (KCl), 0·5 g.; ferrous sulphate ($FeSO_4.7H_2O$), 0·01 g.; sucrose, 30·0 g.; agar agar, 15·0 g.; water to 1000 ml.

(3) *Inorganic A agar:* zinc sulphate ($ZnSO_4.7H_2O$), 0·043 g.; ferrous sulphate ($FeSO_4.7H_2O$), 0·043 g.; ammonium sulphate ($(NH_4)_2SO_4$), 0·17 g.; diammonium hydrogen phosphate ($(NH_4)_2HPO_4$), 5·00 g.; magnesium carbonate ($MgCO_3$), 0·25 g.; potassium carbonate (K_2CO_3), 0·40 g.; normal hydrochloric acid, 52 ml.; glucose, 50·00 g.; agar agar, 15 g.; distilled water to 1000 ml. *p*H 4·5. Nitrogen, 0·12 %.

(4) *Organic C agar:* same as inorganic A, save that monosodium glutaminate (Ajinomoto), 16·00 g., replaced diammonium hydrogen phosphate, and 37 ml. normal hydrochloric acid per litre were required to give *p*H 4·5. Nitrogen, 0·12 %.

Method of inoculation

Three plates of each medium were sown by a central needle point stab from a six-day beer-wort culture of the mould. All strains were sown on the same day, incubated at 24° C. and observed over a period of two weeks. The colonies were studied qualitatively by examination of (*a*) degree of sporing; (*b*) colour of spores; (*c*) type of colony; and quantitatively by measurements of (*a*) all parts of the fruiting structures; (*b*) rate of colony extension.

It is considered that no useful purpose would be served in recording the numerous measurements and observations made in these experiments, and therefore only a brief diagnostic summary has been recorded. Of the twenty strains of blue cheese moulds examined eighteen distributed themselves over three broad classes. The characters distinguishing these classes were significant and constant, but not sufficiently great to dissociate any one strain from the group *P. roqueforti* Thom.

Classification within Penicillium roqueforti *Thom group.*
Colonies on solid media 9 *days at* 24° C.

Class I.

Moulds isolated from Blue Cheshire 1, Blue Cheshire 2, Blue Cheshire 3, Wensleydale.

Diagnosis on:

Inorganic A: Heavily sporing, zonate colony. In Blue Cheshire strains bright green sporing surface.

Czapek-Dox (Thom): Moderately sporing zonate colony with tendency to stellation.

Organic C: Zonate hyphal pattern. Few or no spores.

Class II.

Moulds isolated from French Roquefort 1, French Roquefort 2.

Diagnosis on:

Inorganic A: Thinly sporing, stellate, indefinite colourless edge.

Czapek-Dox (Thom): Lightly sporing, regularly stellate, arachnoid margin.

Organic C: Perfectly regular stellation of mycelial felt. Few or no spores.

Class III.

Moulds isolated from Stilton 1, Stilton 2, Stilton 3, Stilton 4, Stilton 5, Stilton 6, Stilton 7, Gorgonzola 1, Gorgonzola 2, Danish Roquefort, Blue Vinney 1, Blue Vinney 2.

Diagnosis on:

Inorganic A: Heavily sporing, stellate, white hyphal edge, green-blue surface.

Czapek-Dox (Thom): Moderately sporing, irregularly stellate, arachnoid margin.

Organic C: Irregularly stellate, mycelial pattern. Few or no spores.

The growth on beer-wort medium is not recorded, for all colonies were similar to one another except for those falling into class I, which

were distinguishable by their green sporing surface showing slight zonation. It will be noted that the distinguishing features for each class may be grouped as follows:

Table I

Class I	Class II	Class III
Robustly growing strains	Poorly growing strains	Robustly growing strains
Green sporing surface (Ridgway 35′.*k*.)	Green-blue sporing surface Ridgway 37‴.*i*.)	Green-blue sporing surface (Ridgway 37‴.*i*.)
Zonate colony with definite margin	Regularly stellate with indefinite margin	Irregularly stellate with definite margin

The *Penicillium* isolated from Dolce Verde cheese did not belong to the *P. roqueforti* group, and therefore finds no place in the above classification.

Microscopical measurements were taken of specimens from nine-day-old cultures from Czapek-Dox agar plates, mounted in lactophenol. As no striking differences were observed throughout the series, the results have been averaged and recorded as a typical range of variation for each class.

Table II

All measurements in μ

	Conidia	Sterigmata	Metulae	Rami	Penicilli	Conidiophore
Class I	3–4·5	9–10 × 2	9–12 × 3	16–20 × 4	30–50	100–120 × 4–5
Class II	3–5	6–9 × 2	9–12 × 3	12–15 × 3·5	30–50	90–110 × 4–5
Class III	3–6	6–11 × 2	10–12 × 3	15–20 × 3	30–50	100–150 × 4–5
Thom (1930)	4–4·5	Up to 12 × 2–3	12–14 × 4	—	—	100–120 × 4–6

The measurements compared with those of Thom (1930) for *P. roqueforti* Thom are of the same order, and show little or no variation from class to class. It must be concluded, therefore, that all strains under examination are morphologically identical with the type species, *P. roqueforti* Thom, and cannot be separated from one another by microscopical measurements alone.

Pitting of conidiophores and metulae in P. roqueforti *Thom*

Pitting or roughening has generally been accepted as characteristic of certain species of *Penicillium*, and has assumed some diagnostic importance. Certain features of growth observed in this analysis have thrown doubt on the value of pitting as a distinguishing character.

Thom's description of *P. roqueforti* on Czapek agar records "conidiophores roughly granular or pitted (occasionally smooth)", whilst I have found that the walls were consistently smooth when the

moulds were grown on beer-wort medium. When the same strains were cultivated on Czapek agar, a change of the smooth walls to roughened followed with remarkable constancy. A passage experiment, first sowing on Czapek agar, then subculturing on to beer-wort agar, then from beer-wort to Czapek, etc., never once detected a lag in passing from the pitted to the smooth-walled conidiophore, and vice versa.

As growth on Czapek glucose medium is extremely poor (to be discussed under growth requirements) it is suggested that pitting of the conidiophore of *P. roqueforti* is a subtle index of the suitability of the medium, for only under adverse conditions, such as on Czapek agar, does this character appear. It is possible that an author describing a cheese mould may be tempted to create a new variety on his finding smooth-walled conidiophores, when in fact this same mould cultivated on a medium giving poorer growth would possess pitted walls. By way of illustration, Biourge (1923) created *P. stilton* which on wort gelatin possessed smooth walls, but in Thom's laboratory on Czapek agar the same strain was described with pitted conidiophores.

Penicillium roqueforti Thom variety *viride* n.var.

A new variety of *P. roqueforti* Thom has been isolated, belonging exclusively to class I in the above classification, for which the name *P. roqueforti* Thom var. *viride* is proposed. This variety has been consistently isolated from all samples of Blue Cheshire cheese so far examined and has not been found in any other cheese. The character on which this variety is differentiated from *P. roqueforti* Thom is a permanent feature of the mould, is reproducible on any laboratory media and is unaffected by the temperature of incubation:

P. roqueforti Thom var. **viride** n.var. a *P. roqueforti* Thom differt quod viridis clarioris et pigmentum viride in spiritu vini acido solvit.

Distinguished from *P. roqueforti* Thom by its green sporing surface (Ridgway 35′.*k*.) and the solubility of the pigment in acid alcohol.

Specific acid alcohol test. A solution of normal hydrochloric acid (5 ml.) and absolute ethyl alcohol (95 ml.) was prepared. The spores from a five to seven day beer-wort agar slope incubated at 24° C. were washed off with 20 ml. of acidified alcohol and the suspension transferred to a 100 ml. conical flask. The solution was then boiled over gauze for 30 sec. and filtered several times through paper while hot. The spore-free alcoholic filtrate was coloured a deep green resembling a saturated aqueous solution of nickel sulphate.

The test was positive with all strains of *P. roqueforti* Thom var. *viride*; that is, a green filtrate was obtained, whilst with all other strains

in this collection and with other *roquefort* moulds obtained from the collections of Thom, London School of Hygiene, and Baarn, a negative result was universally obtained.

Penicillium of Dolce Verde cheese

The *Penicillium* dominating the fungal microflora of this cheese is interesting, since it is not related to *P. roqueforti* Thom and resembles more *P. expansum* (Link) Thom. Since it appears that no author has previously encountered this type of cheese mould, a detailed description is given here:

Colonies on beer wort, eight days at 24° C., 40 mm. in diam., dense, compact, circular with a white hyphal margin; green-blue sporing surface, fasciculate and coremiform; zonate with radial striations; reverse in shades of brown.

On Czapek solution agar, eight days at 24° C., colonies 40 mm. in diam.; sporing only moderately, sporing areas in sectors, various shades of green; zonate, fasciculate to coremiform; indefinite hyphal edge; reverse in shades of brown to red brown; penicilli asymmetric, 25–36 μ long, variously bi- and triverticillate; conidiophores smooth, 3–3·5 μ wide; rami 10–15 μ long $\times$ 3 μ wide; sterigmata 6–9 μ long $\times$ 2·5 μ wide; conidia globose to subglobose, 3–4 μ in diameter.

Comparing Thom's description of *P. expansum* Thom (1930, p. 406) with the above, the presence of elliptical conidia, and the absence of sectoring in *P. expansum* are the only distinguishing morphological characters.

Discussion

The findings of this investigation point to uniformity of blue cheese moulds in that all, with the exception of the species isolated from Dolce Verde, belong to the *P. roqueforti* Thom group. The dominant mould of Dolce Verde cheese is of paramount interest for two reasons. First, like *P. roqueforti*, it remains viable in the partially anaerobic cavities of the cheese, and secondly, it is related to *P. expansum*, the blue mould associated with the decay of fruit. On this evidence, it appears that the theory of low oxygen-tension survival exclusive to *P. roqueforti* (Thom & Currie, 1913) must be extended to cover also this mould. Furthermore, it is remarkable that a mould related to a food rotting group of organisms should be used to ripen and flavour a cheese.

The fungus of Blue Cheshire cheese has not been recognized previously. Sopp (1912) records a description of *P. aromaticum*

"gammelost" Sopp, which is claimed to be characteristic of the sour-curd type of cheese—Gammelost. He separates this from *P. roqueforti* by its predominantly yellow-green colour (in age) and slight colour in reverse. His descriptions on meat-peptone-sugar-gelatine do not suggest he was dealing with the Blue Cheshire mould.

The classification of strains of the Roquefort group may be based on colony characteristics. That there should be a correlation between class and habitat of the mould invites some comment. In the first place a determining influence must reside in Blue Cheshire cheese which fosters the growth of this "local" mould in preference to the most common variety of *P. roqueforti*. Secondly, that the strain used in the manufacture of French Roquefort cheese has been found in no other cheese is suggestive of a low survival capacity of this strain in surroundings other than in the cheese curd. It has been recorded that this strain is more weakly growing than others on synthetic media. All strains belonging to class III represent those cheeses ripened by the chance inoculation of a "wild" strain of *P. roqueforti* Thom.

Summary

1. The dominant mould of blue cheese is *Penicillium roqueforti* Thom.

2. *P. roqueforti* group may be subdivided on colony characters into three classes.

3. Pitting of conidiophores and metulae is not a stable morphological character in *P. roqueforti* Thom.

4. A new variety has been isolated from Blue Cheshire cheese. The name suggested for this strain is *P. roqueforti* Thom var. *viride*.

5. The dominant mould of Dolce Verde cheese is related to *P. expansum*.

I wish to express my sincere thanks to Prof. H. Raistrick, F.R.S., for his continued interest and valuable advice during the progress of the work. I am also deeply indebted to Mr G. Smith, M.Sc., for his advice, help and criticism in many aspects of this problem. My thanks are due also to the United Dairies, Ltd., whose financial support made this work possible.

Penicillium roqueforti Thom.

6-day beer wort culture. Conidiophore: smooth. Metulae: smooth. Magnification × 1000.

6-day Czapek-Dox culture. Conidiophore: pitted. Metulae: pitted. Magnification × 1000

REFERENCES

Arnaudi, C. (1927). "Sui Penicilli del Gorgonzola." *Boll. Ist. sieroter. Milano*, VI, 13–28.

Biourge, Ph. (1923). "Les moisissures du groupe *Penicillium* Link. Étude monographique." *Cellule*, XXXIII, fasc. 1, 7–331.

Sopp, O. J. Olsen (1912). "Monographie der Pilzgruppe *Penicillium* mit besonderer Berücksichtigung der in Norwegen gefundenen Arten." *Videnskaps. Skrifter*, I, Mat.-Naturv. Klasse, No. 11, X, 208.

Thom, C. (1906). "Fungi in cheese ripening: Camembert and Roquefort." *Bull. U.S. Bur. Anim. Ind.* LXXXII, 1–39.

—— (1930). *The Penicillia.*

Thom, C. & Currie, J. N. (1913). "The dominance of Roquefort mold in cheese." *J. biol. Chem.* XV, 249–58.

Weidemann, C. (1907). "Morphologische und physiologische Beschreibung einiger *Penicillium*-arten." *Zbl. Bakt.* 2. Abt. XIX, 675–690.

Westling, R. (1911). "Über die grünen Spezies der Gattung *Penicillium*." *Ark. Bot.* II, No. 1, 1–156.

ON THE CLASSIFICATION, NOMENCLATURE, HOSTS AND GEOGRAPHICAL RANGE OF *TRAMETES PINI* (THORE) FRIES

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Synonymy

Trametes Pini (Thore) Fries.

Boletus Pini Thore, *Chlor. Land.* 487 (1803); Brot. *Fl. Lusit.* II, 468 (1804).
Polyporus Pini Pers., *Myc. Eur.* II, 83 (1825); Rostk. in Sturm, *Deuts. Fl. Pilze*, IV, 103 (1838).
Daedalea Pini Fries, *Syst. Myc.* I, 336 (1821); *Linnaea*, V, 514 (1830).
Polyporus pinicola b. Berkeley, in Hooker, *The English Flora*, V, 2, 143 (1836).
Trametes Pini Fries, *Epicr. Myc.* 489 (1838).
Daedalea vorax Harkness, *Pacif. Rur. Pr.*, XVII, 4, 49 (1879).
Fomes Pini Karst., "Ryssl. Hattsv.", *Bidr. Finl. Nat. Folk*, XXXVII, 79 (1882).
Fomes Abietis Karst., "Ryssl. Hattsv.", *Bidr. Finl. Nat. Folk*, XXXVII, 242 (1882).
Trametes Abietis Karst., in Sacc. *Syll. Fung.* VI, 346 (1888).
Ochroporus Pini Schroet., *Krypt. Fl. Schles.* III, 487 (1889).
Polyporus piceinus Peck, in *Ann. Rep. N.Y. St. Mus.* XLII, 25 (1889).
Trametes Pini Abietis Karst., "Finl. Basidsv.", *Bidr. Finl. Nat. Folk*, XLVIII, 336 (1889).
Polystictus piceinus Peck, in Sacc. *Syll. Fung.* IX, 187 (1891).
Mucronoporus Abietis Ell. & Ev. *N. Amer. Fungi*, 2507, 2730 (1892); *Fungi Columb.* 1205 (1898).
Xanthochrous Pini Pat., *Cat. Tun.* LII (1897).
Phellinus piceinus Pat., *Tax. Hymén.* XCVII (1900).
Trametes piceinus Peck, in *Ann. Rep. N.Y. St. Mus.* LIV, 169 (1901).
Porodaedalea Pini Murr., in *Bull. Torrey bot. Cl.* XXXII, 7, 367 (1905).
Phellinus pini Ames, in *Ann. mycol., Berl.*, XI, 3, 246 (1913).
Xanthochrous Abietis (Karst.) Bourd. & Galz. *Hymén. de France*, 633 (1927).

History of nomenclature

The history of the classification of *Trametes Pini* is rather involved, as indicated by the foregoing synonymy. This has been largely due to changed concepts, from time to time, of generic identities within

the Polyporaceae, and to various inharmonious redivisions of the older genera. Described first as a *Boletus*, the fungus has since been referred, all told, to ten different genera. The extensive synonymy reveals, moreover, not only nomenclatorial changes and taxonomic difficulties, but genuine confusion of forms found, a confusion which is even yet not entirely dissipated. For the sake of clarification a brief review is desirable.

The earliest description of the plant (1803) is that of Thore, a physician and amateur botanist of Dax. On account of its intrinsic interest, and the fact that it is difficult of access, the description is quoted: "*Bolet—Boletus Pini*, du pin. Nous n'avons pu le rapporter à pas un de ceux décrits dans l'herbier de France. Il est sessile, dimidié, et acquiert jusqu'à six pouces de diamètre; il imite assez bien, par sa forme, un sabot de cheval; il est remarquable par un nombre prodigieux d'enfoncemens circulaires qui en rendent la superficie très-raboteuse; cette superficie est, en outre, légèrement duvetée, surtout les dernières couches, et d'un brun très-foncé et crevacée dans plusieurs endroits. Ses tubes sont roux, extrêmement irréguliers, et disposés par couches. La première est contiguë à la chair qui est très-sèche et très-friable; les autres ne sont que contiguës entre elles. Sa surface inférieure est légèrement concave. Au lieux de tubes, on apperçoit de loin-en-loin des sinuosités aussi irrégulières que les tubes. Nous ne l'avons jamais rencontré que sur les pins, et à toutes les hauteurs."

In an introduction to his treatment of the fungi, Thore acknowledges his debt to Bulliard's *Herbier de France* for names and much descriptive material. But he concluded that his *Boletus Pini* could not be referred to any one of the plants characterized by Bulliard—an opinion which, having seen Bulliard's excellent plates (though not Thore's specimen, for such seems not to have been preserved), I am not inclined to dispute.

Brotero (1804) described the same plant in his *Flora lusitanica*.* No reference is made to Thore, and it may be that the identical name was given independently. Persoon (1825), on transferring the species from the genus *Boletus*, gives *B. Pini* Thore as a synonym for his *Polyporus Pini*,† but makes no reference to the description by Brotero.

* *Boletus Pini* B. Acaulis, pulvinatus; supra fuscus, asper, fasciis elevatis, inaequalibus; subtus lateritius, poris inaequalibus, sublabyrinthiformibus. *Hab.* in Pinis annosis et putrescentibus.

† *Polyporus Pini*, semicylindricus conicus basi dilatatus spadiceus, pileo zonato sulcato-rugoso scabro glabro, margine acuto subtomentoso subtusque cinnamomeo, poris irregularibus distinctis.

Boletus Pini. Thore Chloris Land. p. 487. Hab. prope Dax, in Gallia, ad truncos *Pini rubri*.

Altitudine et latitudine basilari palmaris est. Ad tactum asper. Pori subnitentes, brunnei, magnitudine et forma varii, nonnunquam hinc inde sinulos efformant flexuosos.

On the other hand, Fries's first description (1821), under the name *Daedalea Pini*,* is obviously a transcription of Brotero's. No mention is made of Thore. Later descriptions and notes by Fries (1830, 1883) are original, and longer. In the *Epicrisis*, under the new name *Trametes Pini*, his own *Daedalea Pini*, *Polyporus Pini* Pers., and *Boletus Pini* of Brotero and Thore are all given as synonyms.

Under the name *Polyporus pinicola* Sw., Berkeley (1836) described a variety *b*, with yellow brown margin, large irregular sinuous pores, and tawny flesh, from pine trunks in Scotland. The plant seems referable to *Trametes Pini*. Berkeley states that his account of the fungus is taken from a manuscript by Klotzsch, and that it is on the latter's authority that the specimen then before him is considered a variety of *Polyporus pinicola*. Fries is said to have referred the collection to the latter species, under the name *P. marginatus*; but Berkeley, as indicated, did not agree with this disposition, noting distinct differences between the two. I have been unable to locate the specimen, which is not in the Berkeley collections at Kew. There can be no question as to Klotzsch's (1838) final disposition of the plant, for he gives Berkeley's *Polyporus pinicola b*, in his synonymy of *Daedalea Pini*, in the *Flora Regni Borussici*. The excellent figures and original notes on this fungus leave no doubt in one's mind as to Klotzsch's familiarity with it.

It may be said here that many years later the misdetermination of collections of *Polyporus pinicola* Sw. resulted in the distribution of such specimens *in exsiccati* under the name *Trametes Pini*. Such are found in Thümen Mycotheca Universalis, No. 7, Fungi Austriaci, No. 817, and the Roumeguère Fungi Gallici, Cent. 19, No. 1808. An emended schedule to the Mycotheca Universalis gives No. 7 "*Trametes Pini* Fckl. *Symb. Myc. Nachtr.* 1, 8. *Non Trametes Pini* Fr. *Hymen. eur.* p. 582 *sed Polyporus pinicola* Fr.", and in the Roumeguère exsiccati the specimen is labelled "*Trametes Pini* Fcl. (non. Fr.) Thm. Myc. Univ. No. 7". The specimen in the Fungi Austriaci, however, is labelled *Trametes Pini* Fr.

The source of these errors evidently lies in the misdetermination of specimens collected by Morthier, and distributed by Fuckel under the name *Trametes Pini*. The Fuckel (1871) citation, as given in the Mycotheca Universalis, is incorrect, for there is no reference to *Trametes Pini* on p. 8 of the first supplement to the *Symbolae Mycologicae*, as cited; but on p. 2 (also printed 290, in sequence from the *Symbolae*) we find: "...*T. Pini* Fr. *Epicri.* p. 489. Rost. in St. 4–50 (*Unter Polyporus*) an stammen von *Pinus*, excc. im Winter. Im Jura. (Morthier)." The disposition of the actual specimen or specimens

* *Daedalea Pini* sessilis, pileo pulvinato fusco, fasciis elevatis inaequalibus aspera, poris inaequalibus sublabyrinthif. lateritiis. Bol. pini *Brot. Lusit.* II, 468.
An a prioris b. satis distincta? *Ad Pinus annosas et putrescentes Portugaliae.*

here referred to is unknown, but it is significant, perhaps, that specimen No. 7 of the Mycotheca Universalis was collected by Dr Morthier. On the other hand, specimen No. 817 of the Fungi Austriaci was collected by Thümen himself a few years earlier, and, as noted above, is also a misdetermined specimen of *Polyporus pinicola* Sw. One can only regret the perpetuation of the name *Trametes Pini* Fuck. as a synonym for *Polyporus pinicola* Swartz, in Winter (1884).

Turning next to *Daedalea vorax*, it is to be noted that Harkness (1879) gave this name to a fungus which he found on Douglas fir in western North America. I have examined a specimen of this plant in the Farlow Herbarium, collected and determined by Harkness, and it proves to be the daedaloid form of *Trametes Pini*, a form common on Douglas fir.

Murrill (1905) at first listed *Trametes gausapata* Berk. & Rav. as a synonym of *Porodaedalea Pini*, but later (1908) questioned it. *Trametes gausapata* Berk. & Rav. was described by Cooke (1891) from a collection made by Ravenel in South Carolina, and labelled by Berkeley as *Polyporus gausapatus* Berk. & Rav. Miss E. M. Wakefield has been kind enough to examine the original collection (Ravenel No. 1327) at Kew and informs me that, although the condition of the specimen is such as to render identification impossible, it is not *Trametes Pini*.

One should note, perhaps, the ambiguous *Scindalma Pini* [*canadensis* Schw.] of Kuntze (1898). In reviving Hill's old generic name, Kuntze lists the foregoing among many other transferences from *Polyporus*. What his thoughts and intentions were in respect to this name is not clear, for the position of the bracket (which indicates transference from *Polyporus*) is ambiguous. *Polyporus Pini-canadensis* is synonymous with *Polyporus Pilotae* and *Polyporus croceus*, and is not to be confused with *Trametes Pini*.

The specific epithets *Abietis* and *piceinus* are of considerable interest and importance, for their history reveals curiously parallel cases of confusion as to the identity of forms found in Europe and America. It will be recalled that Thore's description of *Boletus Pini* was drawn from a perennial fructification on pine, and it is applicable only to such. While later descriptions of other authors emphasized the variability of the fungus, they are scarcely applicable to what are now recognized as the extreme *Abietis* forms; and moreover, no hosts other than pine are recorded. Thus it seems very doubtful whether the early mycologists knew the *Abietis* form, or recognized it as *Trametes Pini*. Karsten was the first to describe it, and the history of his experience is interesting.

Karsten (1859) first listed *Trametes Pini* under *Polyporus Pini* Pers. In 1876 he recorded and described it again under the same name, giving *Boletus Pini* Brot. and *Trametes Pini* Fries among other well-known synonyms. The only host given is *Pinus sylvestris*. In 1882 he

placed the plant in the genus *Fomes*, giving the name *F. Pini*, with *Trametes Pini* Fries as a synonym, and also *T. radiciperda* Hart., an error which he later (1882) corrected in an addendum to the publication. In the addendum we also find a new species, *Fomes Abietis* Karst., which he distinguished from *F. Pini* by its softer consistency, its generally more spreading habit, its lighter colour, and its more felty and tomentose top. The host given for this species is the spruce *Picea excelsa*, whereas that of *Fomes Pini* is *Pinus sylvestris*.

In a later treatment of the Polyporaceae, Karsten (1889) changes his disposition of these plants, and describes "*Trametes Pini* syn. *Fomes Pini* Karst. 1882"; and as a variety of the above "*Trametes Abietis* Karst., syn. *Fomes Abietis* Karst. 1882". The exceedingly brief descriptions (referring only to the spores) are identical. The hosts, however, are pine trunks for *Trametes Pini* and trunks and branches of spruce for *Trametes Abietis*.

Turning to *Polyporus piceinus* of Peck we find that this name was applied in 1889 to a soft, small-pored form found on fallen spruce. Later (1901), having seen many more specimens, and become familiar with the often non-*Polyporus*-like habit of the fungus, Peck renamed it *Trametes piceinus*, pointing out the close relationship of the plant to *T. Abietis* Karst., but claiming it to be distinct, on account of alleged differences in pore size, and shape, and in the character of the upper surface of the pileus. Indeed, he recognized some of his collections on decaying pine and spruce wood from New York as *T. Abietis* Karst., remarking that they agreed well with Karsten's description except that "they are scarcely triquetrous, nor are the pores lacerated". So Peck in America had the same experience as Karsten in Europe. Familiar with *T. Pini* as a hard *Fomes*-like fructification on pine, each believed at first, on discovering the soft form on spruce, that he had found a new species; but both came ultimately to recognize a close relationship between these plants.

Lloyd (1915) deals with these forms in his *Synopsis of the Genus Fomes*. His description of *Fomes Pini* (for which nomenclatorial combination he has been wrongly credited) is applicable to those hard and persistent fructifications most characteristic of the hard pines and Douglas fir. He insists that on account of the alleged possession of *Fomes*-like characters this plant should be classified as such. Dealing with "*Trametes Abietis* of Europe" and "*Trametes piceina* of America", he recognizes a close relationship between them and *Fomes Pini*, and is constrained to regard them as *Fomes* species, even though they lack the *Fomes*-like characters of their relative. Lloyd would assign to "*Trametes Abietis* of Europe" only varietal rank under *Fomes Pini*; but he considers *Trametes piceina* Peck distinct on account of supposed differences in pore size and shape.

The present tendency is to regard these forms as belonging to the

same species. Thus, Murrill (1905) includes both under his *Porodaedalea Pini*. One can only regret that it is difficult to recognize in such forms a *Porodaedalea* as defined by Murrill. Overholts (1915) likewise assumes that *Trametes piceinus* Peck and *Fomes Abietis* Karst. are the same. He maintains that *Trametes Pini* var. *Abietis* as distributed by Romell (Fung. Scand. 7) is certainly to be referred to Peck's species. I have examined Peck's type and Romell's collections and I agree with Overholts.* Overholts has also concluded from field observations that *Trametes piceinus* Peck is a form of *T. Pini*. This opinion is held by Lowe (1934) and Shope (1931), although they prefer to place the plant in the genus *Fomes*. Owens (1936, 1936*a*) has recently described a form occurring on *Abies grandis* in Oregon, and has given evidence of the existence of other variants; but in his opinion such are not specifically distinct. A critical study of authentic and type specimens in herbaria, and close observation of the plants under natural conditions in many localities and on various hosts in eastern and western North America, has convinced me that the various forms found represent a single species.

Before closing this brief historical review, reference might be made to the fungus *Trametes Pini* Fr. f. *succinea*, of Conwentz (1890). Mycelia found in amber wood in Oligocene deposits of the Baltic region were so named. Hartig, to whom specimens were submitted, agreed with Conwentz that in all probability this fungus was the same as that which is to-day commonly found on living pines on the Baltic littoral.

Specimens studied

The following herbarium specimens have been studied by the writer:

Trametes Pini (Thore) Fr.

Farlow Herbarium: Fungi Hung. 348 *Trametes Pini* Thore (Linhart); Myc. Mar. 3 *Trametes Pini* Brot. (Zopf & Sydow); Fungi Fenn. 242 *Trametes Pini* Fr. (Karsten); Fungi Estonici Exsiccati 48 *Xanthochrous Pini* (Brot.) Pat. (Lepik); Fungi Scand. 7 *Trametes Pini* (Brot.) Fr. *Abietis Karst.* (Romell); N. Am. Fungi 2507 *Trametes Abietis* Karst. (Ellis & Everhart); N. Am. Fungi 2730 *Macronoporus Abietis* Karst.;

* Through the courtesy of Professor Linkola of the University of Helsingfors, I have been privileged to examine the type of *Fomes Abietis* Karst. This is an interesting specimen showing revived growth and change of orientation, resulting, presumably, from the fall of the host tree. In all other respects it is quite typical of the small irregular bracket fructifications found at the branch stubs of pine, or not uncommonly on spruce. The pores are distinctly of the daedaleoid type. In this respect it differs from Peck's plant which had circular pores characteristic of most (but by no means all) fructifications on spruce. (*Trametes Abietis* Karst. *Finlandia, Mustialu in Tavastia australis*, Sept. 1882, leg. P. A. Karsten).

California Fungi Distr. Herb. Univ. Cal. 286 *Porodaedalea Pini* (Thore) Murr.; spec. ex herb. Univ. Mich. Exped. Isle Royale, Mich. 1930. T.P. 93 *Trametes Pini* (Brot.) Fr. on spruce; spec. ex herb. J. Bresadola *Trametes Pini* (Brot.) Fr. ad truncos *Pini silv.*, Jena, 1890. Coll. Pfeiffer; spec. coll. H. von Schrenk *Trametes Pini* (Brot.) Fr. on trunk of *Pinus echinata*, Carter Co. Mo., 1898; spec. ex herb. F. Buchholz coll. B. 503 *Ochroporus Pini* Schroet., on *Pinus silv.* Weigo, Vesel; spec. coll. Dr H. W. Harkness *Daedalea vorax*, Blue Canyon, Cal., on *Libocedrus*, 1881 (marked "authentic").*

The following are in the Burt Collections in the Farlow Herbarium: Spec. labelled *Polystictus piceinus* Pk., a determination which Burt notes was authenticated by Peck. Spec. labelled *Polystictus piceinus* Pk. 42 Rep. p. 25, similarly authenticated. Burt notes that this specimen elicited the following from Bresadola to whom it was shown: "*Polystictus piceinus* Pk. = *Trametes Abietis* Karst.", and from Ellis: "...the specimen...is *Macronoporus Abietis* Karst".

Herbarium J. H. Faull: Spec. 1635 *Porodaedalea Pini* (Thore) Murr. *Trametes Pini* (Thore) Fries on *Picea*. From Peck's material. *Polyporus piceinus* Peck, Adirondacks, N.Y. State Museum. C. H. Peck (others are labelled *Porodaedalea Pini*); spec. 407, on living *Picea Engelmanni* (Parry) Englm., James River Country, north of Calgary, Alta., August 1914. Coll. F. B. Robertson; spec. 3804, on *Abies arizonica* Merriam, San Francisco Peaks, Arizona, 26 August 1916. W. H. Long (21415); spec. 403 on *Abies lasiocarpa* (Rock) Nutt. Causing heart rot of living trees, also on fallen trunks. Spring Hill. Mont. 3 August 1910. G. G. Hedgcock; spec. 3809, on *Pinus virginiana* Mill. Oakton, Va., 1 February 1913. W. H. Long (19014); spec. 3811, on *Pinus flexilia*, James Elev. 8500 ft. San Francisco Peaks, Arizona, 18 October 1915. W. H. Long (19719).

Arnold Arboretum, Harvard Univ., Pathological Herbarium: Spec. 360, *Trametes Pini* (Brot.) ex Fr. on *Tsuga heterophylla*, Government Camp, Oregon, 1929. G. D. Barker (2865); spec. 1003 *Trametes Pini* (Brot.) ex Fr. on *Pinus Pinaster* Ait., Valley of the Restonico River, near Corte, Corsica. Elev. 3500 ft. Coll. G. D. Barker (3805) 3 April 1932.

Botanical Museum, University of Helsingfors: *Trametes Abietis* Karst. Finlandia, Mustialu in *Tavastia australis*. September 1882, leg. P. A. Karsten.

Hosts and range

Trametes Pini has a wide host range on coniferous forest trees, chiefly within the family Pinaceae. Indeed there are few other hosts, and the occurrence of the fungus on such is rare. For North America,

* See Discussion, p. 185.

Seymour (1929) lists it under the following: *Pinus albicaulis* Engl., *P. Banksiana* Lamb., *P. contorta* Dougl., *P. echinata* Mill., *P. edulis* Engl., *P. flexilis* James., *P. Lambertiana* Dougl., *P. monticola* Dougl. ex Lamb., *P. palustris* Mill., *P. ponderosa* Dougl., *P. resinosa* Ait., *P. rigida* Mill., *P. strobiformis* Engl., *P. Strobus* L., *P. sylvestris* L., *P. taeda* L., *P. virginiana* Mill., *Cedrus Deodara* Loud., *Larix laricina* (Du Roi) Koch, *L. occidentalis* Nutt., *Picea canadensis* (Mill.) B.S.P., *P. Engelmanni* (Parry) Engl., *P. mariana* (Mill.) B.S.P., *P. rubra* (Du Roi) Dietr., *P. sitchensis* Carr., Tsuga *canadensis* (L) Carr., *T. heterophylla* (Raf.) Sarg., *T. mertensiana* (Bong.) Carr., *Pseudotsuga taxifolia* (Lam.) Britton, *Abies arizonica* Merriam, *A. balsamea* (L.) Mill., *A. concolor* Lindl. & Gord. *A. nobilis* Lindl., *Libocedrus decurrens* Torr., *Thuja plicata* D. Don, *Juniperus* (sp. indet.) or "cedar". The fungus is also listed under the hosts *Betula occidentalis* Hook., and *Crataegus* (sp. indet.). In the latter, the authenticity of the determination of the fungus has been questioned by Seymour, in certain instances. The present writer has sought to verify the records of occurrence on hardwoods. Weir (1914) reports finding *Trametes Pini* on *Betula occidentalis*. He refers at the same time to a fungus common on *Crataegus* which might be confused with this, or with *Trametes Abietis* Karst. He considers it specifically distinct, although Lloyd, to whom specimens were sent, called it *T. piceinus* Peck. Shope's (1931) report of *T. Pini* on *Crataegus* is based, according to correspondence with the writer, on specimens presumed to be in the New York Botanical Garden, but I am informed from that institution that no such specimens are there. No specimens supporting Weir's record of occurrence on *Betula* have been located in Washington, and it is perhaps questionable whether they have been preserved.

To the coniferous hosts listed above, others can be added. Thus, according to Meinecke (1914), *Abies grandis* Lindl. is not infrequently attacked. Owens (1936) has recently reported at length on the occurrence of the fungus on this species. It has been collected on *Abies Fraseri* (Pursh) Lindl. (Herb. Univ. Tennessee, No. 1807). I have a specimen from *Pinus radiata* Don, sent by Dr Meinecke, and I have recently collected the fungus from a cedar log (*Thuja occidentalis* L.). Faull (1919) has already reported an instance of *T. Pini* decay caused by this species. From herbarium records, Percival (1933) has given several North American hosts apparently not before published, namely, *Larix Lyallii* Parlat., *Picea Breweriana* S. Wats., and *Pinus clausa* Vasey.

In North America only a few of the important coniferous timber species are free of, or decidedly inhospitable to the fungus. The sequoias, the bald cypress, and the chamaecypari are noteworthy in this regard. There seem to be no records of collections on these trees. The same may be said for several of the western true firs. Yet most, if not all, of these are occasional hosts, and fructifications of the fungus

are probably formed on them under the most favourable circumstances, just as on *Thuja occidentalis*. Thus Boyce (1930) finds that *Abies amabilis* and *A. shastensis*, unrecorded hosts, along with *A. concolor*, *A. grandis*, *A. nobilis*, and *A. magnifica*, are occasionally decayed by *Trametes Pini*, although he says that the *T. Pini* rot is so rare in all these species as to be of little economic importance. The same is said of *Chamaecyparis Lawsoniana*, the Port Orford cedar, and *C. nootkatensis*, which are not given elsewhere as hosts.

It is to the point to refer here to the reported occurrence of *Daedalea vorax* (syn. *Trametes Pini*) on *Libocedrus decurrens*; and to the statements that the fungus is the cause of a serious decay of that species. In Harkness's original account (1879), the fungus is described as "a foe to the lumberman", the cause of a very prevalent heart rot of Douglas fir. In the same paper an exposition is given of a decay of unknown etiology common in the incense cedar. Harkness & Moore (1880) recorded *Daedalea vorax* on *Libocedrus decurrens*. One must presume that it was from this source that Mayr (1890) described *Daedalea vorax* as the cause of a common decay of *Libocedrus decurrens*. Later, Sargent (1896) appears to have followed Mayr in giving a similar account. It appears, however, that *Daedalea vorax* was not found on *Libocedrus decurrens*; for von Schrenk (1900) relates that Harkness assured him in a letter concerning the disease of *Libocedrus*, that the record in the Catalogue of Pacific Fungi was erroneous, and that the host should have been reported as *Abies Douglasii*. Thus *Daedalea vorax* appears in quite familiar guise as a parasite of Douglas fir. There still remains the puzzling rot of the incense cedar, first figured and described by Harkness. This has been investigated by Boyce (1920) who found it to be due to *Polyporus amarus*. Boyce vouches, however, for the occasional occurrence of *Trametes Pini* rot in incense cedar, and records having seen a single fructification of the fungus collected on that species by Weir.

There is some evidence of differences in susceptibility among the various host species liable to *T. Pini* heart rot. Abbot (1915), from a wide experience in Vermont, ranks tamarack as probably the most susceptible species in that State; white pine comes next; and then follow spruce, hemlock and balsam. Von Schrenk (1900) considers tamarack the most susceptible of New England conifers, the spruces follow, and balsam is the most resistant. Hartig (1878) has listed the common north European conifers in the following order: *Pinus sylvestris*, *Larix decidua*, *Picea excelsa*, *Abies pectinata*. An interesting comment is made by von Tubeuf (1906) that in a certain locality where *Pinus Strobus* had been planted, it seemed to be more seriously infected than the native *P. sylvestris*.

Trametes Pini is common in Europe and across Northern Asia, on the important forest conifers mentioned above. It is also known on

L. sibirica Ledeb. (cf. Heikenheimo, 1927). It is reported locally abundant in southern France on *Pinus halepensis* Mill., and *P. maritima* Lamarck (*Pinus pinaster* Soland) (cf. Durand, 1924). It has also been collected in Europe on *P. Cembra* L. and *P. Strobus* L. (cf. Möller, 1904). Tubeuf (1906) records it on *P. montana* Mill. (*P. Mugho* Poir.) and has observed (1905) decay caused by the fungus in yew (*Taxus baccata* L.).

For India, Hole (1914) gives the following hosts: *Pinus excelsa* Wall., *P. longifolia* Roxb., and *Cedrus Deodara* Loud., a list which will doubtless be extended when the Himalayan coniferous forests are more thoroughly explored mycologically.

In the Orient, *Trametes Pini* has been reported on *Picea ajanensis* Fisch., *Abies sachalinensis* Mast., and *Larix dahurica* Turcz., (Hemmi, 1932; von Tubeuf, 1906).

Thus it appears that *Trametes Pini* has a wide host range and a general distribution throughout the coniferous forest regions of the northern hemisphere. In the southern hemisphere, with one exception which is of questionable authenticity, there appears to have been no collections of the fungus on conifers or other hosts. Cooke (1892) reported it briefly "on trunks, in West Australia". McAlpine (1895) has repeated this record of Cooke's, but Cleland and other students of the Polyporaceae have never discovered the fungus in Australia or New Zealand, and it is unknown in those countries to mycologists who have recently written to me (Cunningham, Young).

Its natural occurrence in South Africa seems improbable because of the absence of native conifers; nor does it seem to have been introduced, for there is no record of its occurrence either on any native tree or on any of the numerous conifers introduced for forest planting. (Cf. van der Bijl 1922, 1929; Doidge & Bottomley 1931). Similarly, for South America, I have failed to find among the scattered papers dealing with mycological collections, any record of the fungus.

I have recently seen records of the occurrence of *Trametes Pini* as follows: On *Picea Schrenkiana* Fisch. & Mey, Pilat, A., "Additamenta ad floram Sibiriae, Asie centralis orientalisque mycologicam. Pars quarta." *Bull. Soc. mycol. Fr.* LII, 3, 317 (1936). Liubarskii reports the occurrence of the fungus in *Picea jezoensis* Carr., *P. obovata* Ledeb. *Pinus koraiensis* Sieb. & Zucc., *P. sylvestris* L., *Larix dahurica* Turcz., *L. olgensis* Henry. Liubarskii, L. V. ("The pine fungus *Trametes Pini* in the far eastern region.") *Bull. Far East. Branch Acad. Sci. U.S.S.R.* XXI, 113–123, f. 1–5 (1936). In correspondence with me, R. Imazeki, of Tokyo, says that *Trametes Pini* is one of the most destructive forest parasites of many conifers in northern Japan, including *Pinus densiflora* Sieb. & Zucc., *Abies firma* Sieb. & Zucc., *Larix Kaempferi* Sarg., *Picea jezoensis* Carr., *P. jezoensis* var. *hondoensis* Rehd., *Tsuga Sieboldii* Carr.

REFERENCES

Abbott, F. H. (1915). "The red rot of conifers." *Bull. Vt agric. Exp. Sta.* No. 191.

Berkeley, M. J. (1836). "The fungi" in Hooker, *English Flora*, II, 43.

Bijl, P. A. van der (1922). "A contribution to our knowledge of the Polyporaceae of South Africa." *S. Afr. J. Sci.* XVIII, 246.

—— (1929). "Fungous Flora of the Western Province of the Cape," in *The Botanical Features of the S.W. Cape Province, Cape Town*. 99.

Boyce, J. S. (1920). "The dry-rot of incense cedar." *Bull. U.S. Dep. Agric.* No. 871.

—— (1930). "Decay in Pacific north-west conifers." *Bull. Yale Univ. Osborn Bot. Lab.* No. 1.

Brotero, F. A. (1804). *Flora lusitanica*, 468.

Cooke, M. C. (1891). "*Trametes* and its allies." *Grevillea*, XIX, 102.

—— (1892). *Handbook of Australian fungi.*

Conwentz, H. (1890). *Monographie der baltischen Bernsteinbäume.*

Doidge, E. M. & Bottomley, A. M. (1931). "A revised list of plant diseases occurring in South Africa." *Mem. bot. Surv. S. Afr.* XI.

Durand, J. P. (1924). "Le *Trametes* du pin." *Rev. Eaux For.* LXII, 59.

Faull, J. H. (1919). *Report of the Minister of Lands, Forests and Mines, Ontario*, p. 125.

Fries, Elias (1821). *Systema mycologicum*, 336.

—— (1830). "Eclogae fungorum, praecipue ex herbariis Germanorum descriptorum." *Linnaea*, V, 514.

—— (1883). *Epicrisis systematis mycologici seu synopsis Hymenomycetorum*, 489.

Fuckel, L. (1871). *Symbolae mycologicae. Beiträge zur Kenntniss der Rheinischen Pilze. Erster Nachtrag.*

Harkness, H. W. (1879). "A foe to the lumberman." *Pacif. Rur. Pr.* XVII, 49.

Harkness, H. W. & Moore, J. P. (1880). *Catalogue of Pacific fungi. Calif. Acad. Sci.* San Francisco, XII.

Hartig, R. (1878). *Die Zersetzungserscheinungen des Holzes.*

Heikenheimo, O. (1927). "Über die Sturmschäden in dem Lärchenwalde bei Raivola am 23 September 1924 (Referat)." *Commun. Instit. Quaestion. Forestal. Finlandiae*, XII, 5.

Hemmi, T. (1932). "Studies in some wood destroying fungi attacking conifers in Japan." *Mem. Coll. Agric. Kyoto*, XX, 20.

Hole, R. S. (1914). "*Trametes Pini* Fries in India." *Indian For. Rec.* V, 159.

Karsten, P. A. (1859). *Sydvestra Finlands Polyporeer*, 43.

—— (1876). "Mycologia Fennica. III. Basidiomycetes." *Bidr. Finl. Nat. Folk*, XXV, 278.

—— (1882). "Rysslands, Finlands och den Skandinaviska Halföus Hattsvampar." *Bidr. Finl. Nat. Folk*, XXXVII, 79, 242.

—— (1889). *Kritisk öfversigt af Finlands Basidsvampar* (Basidiomycetes: Gastero- et Hymenomycetes). Helsingfors.

Klotzsch, F. (1838). In Dietrich, *Flora Regni Borussici*, 380.

Kuntze, C. E. O. (1898). *Revisio generum plantarum*, III, 519.

Lloyd, C. G. (1915). "Synopsis of the genus *Fomes*." *Mycological Writings*, IV, 274.

Lowe, J. L. (1934). "The Polyporaceae of New York State (Pileate species)." *Tech. Bull. N.Y. St. Coll. For.* No. 41.

Mayr, R. (1890). *Die Waldungen von Nordamerika*, 324.

McAlpine, D. (1895). *Australian Fungi.*

Meinecke, E. P. (1914). "Forest tree diseases common in California and Nevada." *U.S. Dep. Agric. For. Ser. Manual.*

Möller, A. (1904). "Über die Notwendigkeit und Möglichkeit wirksamer Bekämpfung des Kiefernbaumschwammes *Trametes Pini* (Thore) Fries." *Z. Forst- u. Jagdw.* XXXVI, 677.

Murrill, W. A. (1905). "Polyporaceae of North America." *Bull. Torrey bot. Cl.* xxxii, 368.
—— (1908). "Polyporaceae." *North Amer. Flora*, ix, ii, 111.
Owens, C. E. (1936). "Studies on the wood-rotting fungus *Fomes Pini*. I. Variations in morphology and growth habit." *Amer. J. Bot.* xxiii, 144.
—— (1936*a*). "Studies on the wood-rotting fungus *Fomes Pini*. II. Cultural characteristics." *Amer. J. Bot.* xxiii, 235.
Overholts, L. O. (1915). "Comparative studies in the Polyporaceae." *Ann. Mo. bot. Gdn*, ii, 667.
Peck, C. H. (1889). In *Ann. Rep. N.Y. St. Mus.* xlii, 25.
—— (1901). In *Ann. Rep. N.Y. St. Mus.* liv, 169.
Percival, W. C. (1933). "A contribution to the biology of *Fomes Pini* (Thore) Lloyd (*Trametes Pini* (Thore) Fries.)." *Tech. Publ. N.Y. St. Coll. For.* No. 40.
Persoon, C. H. (1825). *Mycologia europaea*, ii, 83.
Sargent, C. S. (1896). *The Silva of North America*, x, 134.
Schrenk, H. von (1900). "A disease of *Taxodium distichum* known as peckiness, also a similar disease of *Libocedrus decurrens* known as pin-rot." *Ann. Rep. Mo. bot. Gdn*, xi, 24.
—— (1900*a*). "Some diseases of New England conifers." *Bull. U.S. Div. Veg. Physiol. Path.* No. 25.
Seymour, A. B. (1929). *Host Index of the fungi of North America.*
Shope, P. F. (1931). "The Polyporaceae of Colorado." *Ann. Mo. bot. Gdn*, xviii, 287.
Thore, J. (1803). *Essai d'une chloris du departement des Landes*, 487.
Tubeuf, K. von (1905). "Eine vom Specht geringelte Eibe." *Z. Land. Forstw.* iii, 511.
—— (1906). "Notizen über die Vertikalverbreitung des *Trametes Pini* und ihr Vorkommen an verschiedenen Holzarten." *Z. Land. Forstw.* iv, 96.
Weir, J. R. (1914). "Notes on wood destroying fungi which grow on both coniferous and deciduous trees. I." *Phytopathology*, iv, 272.
Winter, C. (1884). "Die Pilze," in Rabenhorst, *Krypt.-Flora*, i, 422.

CLADOSARUM OLIVACEUM. A NEW HYPHOMYCETE

By EDWARD YUILL and JOHN L. YUILL

(With Plates XI–XIII)

The fungus which is the subject of this communication is of unusual interest in having marked structural differences from its nearest allies, and in raising important questions as to its origin.

Cladosarum olivaceum was first found in December 1935 growing in a culture of *Aspergillus niger*, covering an area of about 2 sq.cm., differing enough in colour and appearance from the black mould to arrest attention.* Up to that time in the course of the routine examination of well over a quarter of a million cultures of *A. niger*, no other mould, obviously different from known species, had been found. The new mould has subsequently been found in two other cultures of the same strain of *A. niger*; two heads only were present in each culture (Pl. XI, fig. 1). The possibility of these occurrences being due to air-borne spores is considered below.

Isolation

The first specimen was subcultured on a variety of media and gave cultures still mixed with *Aspergillus*, which on further subculturing was eliminated.

The colour of the isolated mould varied considerably with the medium used but was generally some shade of greenish olive to gray; under the hand lens or with the unaided eye it closely resembled an *Aspergillus* (section: Euglobosae-Blochwitz).

From the subcultures several colonies were grown from isolated single conidia.

Culture methods

The mould grows well on all usual culture media. Beer-wort agar and bread give good cultures, and the synthetic medium used by Kardo-Ssyssojewa (1936) with the addition of 1½ % agar is very satisfactory.†

* Acknowledgement is due to an assistant, Robert Mason, who submitted the "infected" culture in the first instance for examination.

† This medium contains:

NH_4NO_3	0·3 %	$ZnSO_4$	0·02 %
KH_2PO_4	0·1 %	$FeSO_4$	0·02 %
$MgSO_4$	0·1 %	Sucrose	20 %

On such media, however, growth is too rampant to give the best material for microscopic studies. For this purpose plain agar (1½ %) was found suitable, and colonies grown on this medium were used in the study of the general morphology of the mould. Plain agar gives slow-growing and restricted colonies which can be examined alive under the low powers of the microscope. Foot cells, anastomoses, and the early stages of head formation are thus more easily observed than is possible when richer growths are used. Colonies can be grown to the required stage, on thin layers of this medium in Petri dishes, and can safely be examined with the lids removed, as infection by air-borne spores rarely gives rise to visible colonies before the culture has served its purpose. Selected areas of colonies can be mounted temporarily with a cover glass after applying a few drops of lactophenol. Pl. XII, fig. 10 is from a photograph of a mount of this type.

Small portions from normal vigorous colonies were removed with a pair of fine forceps and prepared for examination by flooding with methylated spirit on a slide and mounting in lactophenol. The addition of cotton blue or picric acid to the lactophenol was sometimes used with advantage. Slides prepared in this way are reasonably permanent if the cover glasses are ringed with cement.

To permit examination of the internal structure of the heads after pigmentation has set in, it is advisable to clear with normal caustic potash. Two or three applications of the alkali remove the pigment, a further drop is then applied to serve as a temporary mounting fluid. The lightest pressure on the cover glass is enough to disperse the structures of the head without causing any damage. Von Höhnel (1916) used this treatment to elucidate the complicated structure of the spore head of *Cristulariella depraedans* (Cooke) v. H. It is an advantage for photomicrographic work to add a little cotton blue to the alkali and to filter before use.

None of the foregoing methods is of much use for making observations of the spores *in situ*. All the usual mounting media which were tested washed the spores away from the heads. This difficulty was overcome by mounting the heads in medicinal paraffin or in linseed oil.

The spores are recognizable under the 8 mm. objective, which is useful for selecting suitable heads for more critical inspection.

Colony characteristics

The colonies grow well on most solid media at temperatures from 18 to 37° C. Gelatine is liquified in six days at 20°.

Czapek solution agar. The colonies resemble those of *Aspergillus niger*, particularly in the early stages; the mycelium is often sulphur-yellow, especially at room temperature, and the general colony colour grey to

greenish black, becoming grey-black with age; the reverse is either uncoloured or light chrome-yellow; the medium is not coloured. Under a hand lens the young heads show a peculiar lustre which diminishes with age. (Pl. XI, fig. 2). The colonies are wrinkled and frequently fringed with a zone of aerial hyphae. Drops of brown-black exudate are generally found among the herbage. In old colonies small new heads grow from those first formed (Pl. XI, fig. 4). Oxalate crystals are formed freely in the medium.

Potato plugs. The colonies are greenish olive, becoming brown-black with age. Sclerotia are produced, as by many strains of *A. niger*. They are globose, 1–1·5 mm. in diameter, creamy white.

Bread slices. The colony is greenish olive, later becoming nearly black. Sclerotia are frequent. Very old cultures sometimes show bunches of radiating needle-shaped crystals of ammonium oxalate arising from the mycelium and from the heads (Pl. XI, fig. 3).

Nutrient gelatine. The mould liquifies gelatine readily, the liquified medium becoming deep brown-black. Ammonium oxalate crystals are later found in the liquid.

Beer-wort agar. The colony is greenish olive.

Morphology

The vegetative mycelium consists of septate, branching, hyaline hyphae, often anastomosing by "bridge" or H pieces (Pl. XII, fig. 10). Conidiophores (stalk and head) arise as branches from clearly differentiated foot cells. The stalks are perpendicular to the long axis of the foot cells; they are at first hyaline, later becoming filled with brown-black pigment; they measure 1·5 mm. high × 15 μ, are unseptate and have a smooth surface.

The vesicle develops from the top of the stalk which is at first quill-like. The tip swells until it becomes globose, then the outer surface becomes closely covered with wart-like protrusions which grow outward into structures similar to the primary sterigmata of *A. niger*. Dark pigment is rapidly produced in the vesicle, and then in the cells growing from its surface. The vesicle averages 70 μ in diameter with a wall 3 μ thick. The sterigmata are very variable from head to head; 16 × 3·5 μ may be given as an average measurement.

Up to this point in development there is little to distinguish the new mould from *A. niger*. The next cells to appear, one to four from each primary sterigma, probably correspond to the secondary sterigmata of *A. niger* but do not give rise to chains of conidia.

They produce instead, septate branching outgrowths of irregular form in which bulbous and flask-shaped elements are common. Branching appears to occur wherever space allows and results in a

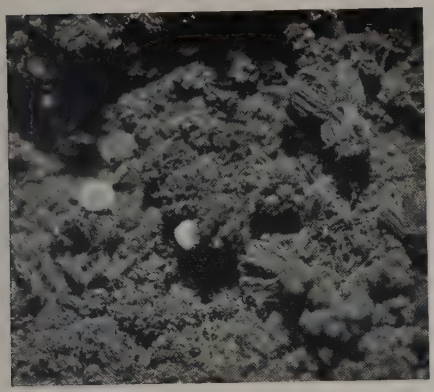

Fig. 1

Fig. 2

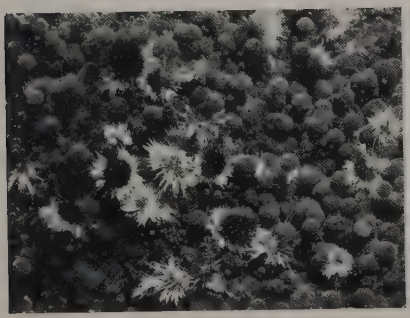

Fig. 3

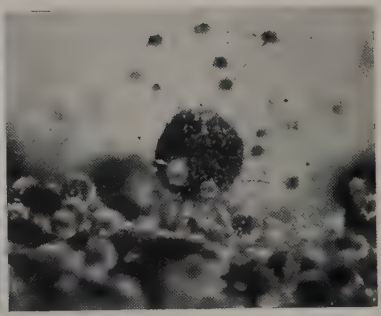

Fig. 4

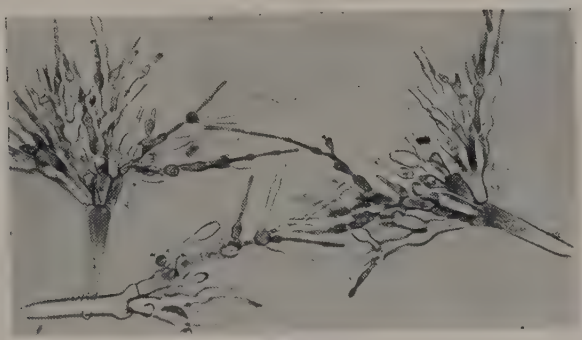

Fig. 5

spherical head, of average diameter 450 μ (Pl. XIII, fig. 14), very closely packed, and never splitting into columnar sections such as are met with in the mature heads of *A. niger* (Pl. XI, fig. 1). The same head normally presents every gradation of complexity in the branching system, ranging from apparently abortive simple outgrowths to those which are repeatedly verticillate. Young branch systems often recall the structures characteristic of *Penicillium*.

Some of the branches—comparatively few—develop a single, generally terminal conidium. This is spherical, 4–5 μ in diameter, dark brown and has a smooth surface (Pl. XII, figs. 8, 9). Though hitherto these conidia have been found singly, it cannot be excluded that under other conditions, more might be developed from the same cell.

Single conidia have been detached by a modification of the Dickinson method of micro-manipulation (1933), placed on Czapek solution agar, and germination, colony formation and fruiting observed. The spore first swells to two to three times its original size and sends out one or two germ tubes which rapidly become septate and branch, so forming a colony which in two or three days at 28° C. produces the characteristic greenish black heads.

The new mould differs from *Aspergillus* principally in the development of a system of branched outgrowths from the sterigmata and in failing to produce chains of conidia. These two important differences place the mould outside the limits of the form genus *Aspergillus*, and appear to necessitate the creation of a new form-genus of which this species is the type.

The name proposed for the new mould is *Cladosarum olivaceum* (Greek, *Klados* = branch—from the branched structures arising from the sterigmata. Greek, *Saron* = brush—to retain the idea behind *Aspergillus*, a little brush. The specific name refers to the colour of the mould grown on bread).

Discussion

It is difficult to avoid the impression that this mould is related to *Aspergillus niger*. Direct evidence as to its origin, however, is entirely lacking. It is possible that *Cladosarum* was derived in some unknown way from the culture of *A. niger* in which it appeared, or it may have been a chance contamination.

Our experience with many cultures of this mould shows that the chances of air-borne contamination are more remote than usual. Although no precautions have been taken to prevent it contaminating other cultures prepared in the same room, such contamination has never occurred, either in tubes or Petri dishes. This is a result which would not be expected. It may be explained partly by the comparative

rareness of the conidia and partly by the fact that they are not easily detached. We have found that the conidia may be washed off but that they are not dislodged by air currents.

As to the alternative possibility that *Cladosarum* was derived from *Aspergillus niger*, there are a number of facts pointing in its favour, in addition to the degree of morphological similarity to *A. niger* already described.

As stated in the introduction, *Cladosarum* has so far appeared three times, each time in a tube culture of the same strain of *Aspergillus niger*.

The Aspergilli are well known to be an unstable group of moulds; a number of mutations have been reported from time to time.* *A. niger* itself is recognized as being the name of a group of closely related black moulds rather than of a single species (Thom & Church, 1926). Several instances of mutation by *A. niger* are already known (Schiemann, 1912). One would not, therefore, be unprepared to meet another example of mutation. It must be admitted that the morphological differences between *Cladosarum* and *Aspergillus niger* go far beyond those associated with previously described mutants. A search of the literature has failed to disclose any description of a mould like the present, whether derived from *Aspergillus* or not.

Cladosarum shows to a striking extent the biochemical activities of *Aspergillus niger*. Thus when grown on a sugar solution in acid conditions, it converts much of the sugar into citric acid and, on a similar solution in the presence of chalk, it produces mainly gluconic acid. Under other conditions, it converts sugar into oxalic acid and in acid cultures, the presence of mould starch (Schmidt, 1925) can be demonstrated both in the mycelium and in the liquid.

There is thus some evidence that an origin from *A. niger* is not improbable. No cytological comparison of the two moulds has yet been undertaken.

Since its isolation, *Cladosarum* has been kept in continuous cultivation by mass transfers on tubes and has maintained its characteristics unchanged throughout a period of over two years.

Systematic position

So far, the new fungus is known only in its conidial stage, and apart from the presence of sclerotia there is nothing to suggest that an ascosporic stage may eventually be found. Brefeld (1876) reported ascospore production from the similar sclerotia of *Aspergillus niger* but no later worker has been able to confirm this claim.

As a conidial form, therefore, *Cladosarum* must be given a position in the Fungi Imperfecti. The obvious affinities it has with the Aspergilli

* For a recent review of a number of instances, Barnes, B., Presidential address, *Trans. Brit. mycol. Soc.* xx, 17–32, may be consulted.

indicate that the section including *Aspergillus* and *Penicillium* would also be appropriate for the new form-genus.

It is therefore proposed that *Cladosarum* should be referred to the Section Aspergillae near to *Aspergillus*, of the family Moniliaceae and order Moniliales Sacc.

Generic diagnosis

Vegetative mycelium of septate, branching, hyaline hyphae sometimes producing sclerotia. Conidial apparatus developed as stalks and heads from enlarged thick-walled hyphal cells (the foot cells) producing stalks as branches perpendicular to the long axis of the foot cells. Stalks terminating in fertile vesicles bearing sterigmata, from each of which arise one to several repeatedly branching septate outgrowths. Single conidia borne sparsely at or near the ends of the branched outgrowths.

Specific diagnosis

Colonies grey to greenish black, reverse uncoloured or light yellow. Stalks 1·5 mm. × 15 μ, smooth, non-septate, at first uncoloured, later filled with dark pigment. Vesicle 70 μ spherical. Sterigmata covering the whole surface. Primary sterigmata 16 × 3·5 μ bearing 1–4 secondary sterigmata, 10 × 3 μ. The latter produce septate branching outgrowths which result in a closely packed head of 450 μ average diameter. Single conidia sparsely developed usually at or near the ends of the branched outgrowths.

Conidia are spherical, dark brown, smooth, 4 μ diameter.

Sclerotia occasionally produced: creamy-white, spherical, about 1–1·5 mm. diameter.

Colonies quickly liquify gelatine.

Cladosarum E. & J. L. Yuill n.g.

Mycelium vegetativum et conidiophororum initia *Aspergillo nigro* persimilia. Conidiophora globosa, sterigmatibus ornata. Sterigmata in hyphis ramosis septatis producta. Conidia singula ad ramulos terminalia vel subterminalia.

Cladosarum olivaceum E. & J. L. Yuill n.sp. Caespitibus griseis vel virido-nigris; conidiophoris copiosis, stipite levi, inseptata, primum hyalina deinde fuscescente, vesicula spherica terminatis; sterigmatibus vesiculam dense contegentibus; sterigmatibus primariis 1–4 levibus, secundaria ornatis; conidiis singulis, sphericis, fuscobrunneis, diametro 4 μ; sclerotiis (sed rare generatis) sphaericis, lacteis, diametro 1–15 μ.

Per vegetationem huius speciei gelatina liquescit.

Summary

A new fungus originally isolated from cultures of *Aspergillus niger* is described. Its morphology is similar to that of *A. niger* until after the production of sterigmata, when its development follows an entirely different course. This necessitates the provision of a new form-genus, for which the name *Cladosarum* is proposed. The possibility of its origin from *Aspergillus niger* is discussed.

Acknowledgements

We are indebted to a colleague, Mr G. H. Gossop, for much help with the culture work and assistance with the microscopical studies. We desire to thank cordially Dr J. Ramsbottom for advice and facilities for consulting the literature, for examining the fungus and also for helping with the Latin diagnoses. Our thanks are also due to the Directors of Messrs John and E. Sturge (Citric), Ltd., for permission to publish this account of work done in their laboratories.

REFERENCES

Brefeld, O. (1876). *Bot. Ztg*, xxxiv, 265.

Dickinson, Sidney (1933). "The technique of isolation in microbiology." *Phytopathology*, xxiii, 365–6.

Höhnel, Franz von (1916). "Fragmente zur Mykologie. XVIII. Mitteilung, Nr. 944 bis 1000." *S.B. Akad. Wiss. Wien*, Abt. 1, cxxv, 27.

Kardo-Ssyssojewa, H. (1936). "Acid formation and acid resistance of *A. niger*." *Z. Bakt.* xciii, 264.

Schiemann, E. (1912). "Mutationem bei Aspergillus niger Van Teighem." *Z. indukt. Abstamm. -u. VererbLehre*, viii, 1.

Schmidt, D. (1925). *Biochem. Z.* clviii, 223–252.

Thom, C. & Church, M. B. (1926). *The Aspergilli*, p. 170.

EXPLANATION OF PLATES XI TO XIII
CLADOSARUM OLIVACEUM

Plate XI

Fig. 1. Two heads of *C. olivaceum* (light heads to left of middle of field) in a culture of *A. niger*. × 13. Photographed from living culture.
Fig. 2. Part of colony of *C. olivaceum* on wort agar. × 17.
Fig. 3. Old culture showing ammonium oxalate crystals. × 4.
Fig. 4. Old head producing small young heads. × 30.
Fig. 5. Sterigmata and branched system from immature head. × 425.

Plate XII

Fig. 6. Young head and dispersed portions from other heads. × 190.
Fig. 7. A terminal portion of branch system from a mature head. × 425.
Fig. 8. A terminal conidium. × 790.
Fig. 9. Another terminal conidium. × 790.
Fig. 10. Foot cell, stalk and head. × 190. H pieces are seen in the mycelium. Photographed from culture on plain agar medium in Petri dish.

Plate XIII

Fig. 11. Early stages in growth of vesicle and primary sterigmata. × 190.
Fig. 12. More advanced stages in development of sterigmata. × 190.
Fig. 13. Heads with sterigmata just developing branches. × 100. Slide cleared with bleaching powder solution.
Fig. 14. A small mature head. × 100. Photographed from living culture in Petri dish.

Fig. 6

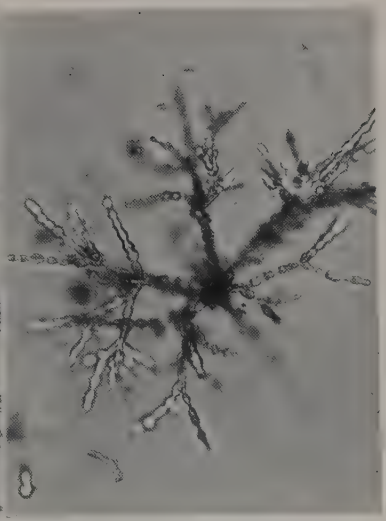

Fig 7

Fig. 8

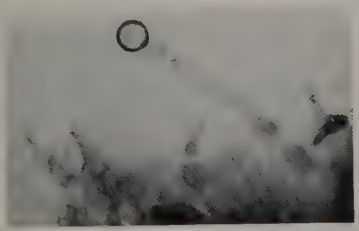

Fig. 9

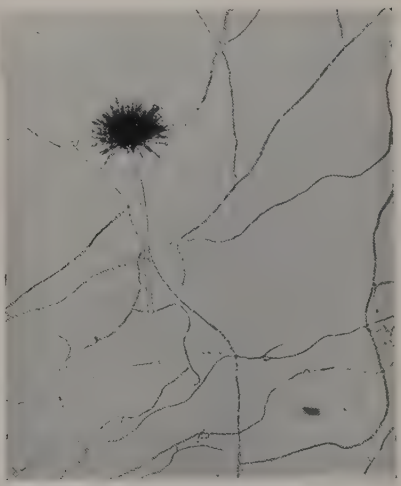

Fig. 10

Fig. 11

Fig. 12

Fig. 13

Fig. 14

SCLEROTINIA POLYBLASTIS N.SP. ON NARCISSUS THE PERFECT STAGE OF *BOTRYTIS POLYBLASTIS* DOWSON

By P. H. GREGORY

(*Seale-Hayne Agricultural College, Newton Abbot, Devon*)

Drayton in 1937 showed that *Botrytis convoluta* has as its perfect stage a *Sclerotinia* which he named *S. convoluta*. He also concluded from a survey of the relevant literature that three other instances of such an association between a *Botrytis* and a *Sclerotinia* are well established by careful work with cultures: *S. Geranii*, *S. Ricini* and *S. Porri*. It is therefore of interest to record a further instance of the connexion between a *Sclerotinia* and a *Botrytis* which came under observation recently.

In February 1938 abundant apothecia of a *Sclerotinia* were observed in the Isles of Scilly on over-wintered leaves of narcissus "Soleil d'Or" which had been killed in the summer of 1937 by "fire" due to *Botrytis polyblastis* Dowson. Apothecia were brought into the laboratory and allowed to shoot ascospores up on to sterile films of agar on glass slips. Fifty-four single ascospores were isolated in hanging drops of agar by Hanna's wet-needle method. Nine of these spores germinated and were transferred to agar slants, the other forty-five did not grow and the drops remained sterile.

As a result of the following observations on these cultures from single ascospores it is concluded that there is a genetic connexion between this *Sclerotinia* and *Botrytis polyblastis*.

(1) The ascospore cultures on prune agar and oatmeal agar resemble in general appearance those from single conidia of *B. polyblastis*.

(2) This resemblance holds for microscopic characters, particularly the production in sporodochia of immense numbers of slimy phialospores (microconidia) which appear to be incapable of germination.

(3) Neither these ascospore cultures from the *Sclerotinia* nor conidial cultures of *Botrytis polyblastis* produce conidia of *Botrytis* under conditions so far tested. Healthy uninjured Narcissus flowers in moist dishes were inoculated therefore from each of the cultures derived from single ascospores. After eight days large conidia, up to 60 μ in diameter, characteristic of *B. polyblastis*, developed profusely on necrotic lesions around the site of the inoculation, while parts of the same flower remote from the inoculum remained healthy. When

placed in water these conidia germinated with from six to eight germ-tubes. Inoculations with multi-ascospore cultures yielded similar conidia.

(4) Isolations of single conidia produced on these inoculated flowers again produced cultures typical of *B. polyblastis*.

The extraordinary characters of the conidia of *B. polyblastis* make it easy to distinguish from the ubiquitous strains of *B. cinerea*. Further the absence of conidia except on the host tissue renders *B. polyblastis* unsuccessful as a laboratory contaminant.

It is concluded that the *Sclerotinia* collected in the field is the perfect stage of *Botrytis polyblastis* and it is accordingly named *Sclerotinia polyblastis*.

Sclerotinia polyblastis sp.nov.

Conidial stage: *Botrytis polyblastis* Dowson, in *Trans. Brit. mycol. Soc.* XIII, 102, 1928.

Apothecia arising from sclerotia singly or in groups, burnt umber-brown, scantily pubescent; disc cyathiform becoming discoid, 3–4 mm. diam.; stipe 3–8 mm. long, 2 mm. diam. below the cup tapering to 0·5 mm. at base, burnt umber-brown, blackish at base; excipulum thin. Asci cylindrical 150–170 × 7–10 μ. Ascospores 8, uniseriate, ellipsoid, non-septate, hyaline, biguttulate, normally 14–20 × 7–10 μ, but often a proportion abortive 10–14 × 6–10 μ. Paraphyses straight, filiform, septate, 1·5–3 μ diam., tips clubbed 4 μ diam., or somewhat irregular or even forked.

Sclerotia black 3–8 mm. long, 1·5–3 mm. wide, 1–1·5 mm. thick, flattened, elongated-oval, embedded in leaf.

Habitat: on over-wintered leaves of *Narcissus tazetta* var. "Soleil d'Or" at St Mary's, Isles of Scilly, England; known also from St Hilary, Cornwall, England.

Conidial stage: *Botrytis polyblastis* Dowson causing a disease of flowers and leaves of narcissus.

Type specimen deposited in the Herbarium, Royal Botanic Gardens, Kew, England.

Apothecia brunnea, leviter albo-pubescentia, e sclerotiis singula vel aggregatim (1–5) oriunda, discis cyathiformibus tandem planis, 3–4 mm. diametro; stipites concolores, ad basim versus nigrescentes, 3–8 mm. alti, sursum ad 2 mm. crassi, deorsum attenuati. Asci cylindrici 150–170 × 7–10 μ. Ascosporae 8, monostichae, hyalinae, ellipsoideae, continuae, biguttulatae, 14–20 × 7–10 μ, quaedam saepe abortivae 10–14 × 6–10 μ. Paraphyses septatae, 1·5–3 μ diametro, apicibus plerumque clavatis, 4 μ aut interdum irregularia vel furcata. Sclerotia immersa, nigra, elongato-ovoidea, complanata, 3–8 mm. longa, 1·5–5 mm. lata, 1–1·5 mm. crassa.

Hab. In foliis hibernantibus Narcissi Tazettae, St Mary's, Insulis Scilloniis, Brittania.

Status conidicus est *Botrytis polyblastis* Dowson, in Narcissi foliis floribusque maculas efficiens.

I would like to thank Miss E. M. Wakefield, M.A., F.L.S., for kindly supplying a Latin diagnosis.

In due course it is hoped to present a more detailed study of the many interesting features presented by this fungus. This work has been carried out at Seale-Hayne Agricultural College with the help of grants from the Great Western Railway Company through the Cornwall Farmer's Union, and from the Ministry of Agriculture and Fisheries.